PHOTINUS COLLUSTRANS: REPRODUCTIVE ECOLOGY OF
FLIGHTLESS FEMALE FIREFLIES
(COLEOPTERA: LAMPYRIDAE)

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
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Earth angel, earth angel

will you be mine?

The Penguins

ACKNOWLEDGEMENTS

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Chairman: James E. Lloyd
Major Department: Entomology and Nematology

Characteristics of Photinus collustrans fireflies, more fully

revealed here, allowed me to address topics in animal reproductive

ecology that had previously been investigated in few, or no, species in

the field.

Female collustrans are flightless and live in burrows in the soil.

They leave these burrows only for mating, and almost all females mate

only once. While outside of the burrow, females are more likely to be

attacked by predators than when in the burrow. The more nights it takes

for a female to mate, the fewer eggs she will deposit.

On the first night a female leaves her burrow, her exit coincides

with the nightly peak in numbers of searching males. On subsequent

nights, females that are still unmated exit earlier and so are available

during more of the male searching period. Females that are

unmated at the end of the male searching period for that evening may

remain outside the burrow long after male search has ended.

The brachypterous females of collustrans are less mobile and more

semelparous than either the alate females of other Photinus species or

the larviform females of Phausis reticulata. These chapters provide a

detailed description of an extremely limited adult role in a female

insect. This provides a base line case for comparison with other insect

species.

INTRODUCTION

> . . . there are two tribes of biologists. One is
> devoted to solving some fundamental problem or other by
> looking around for the right organism with which to
> accomplish the trick. The other, to which I belong, is
> devoted to glorifying their favorite organism . . . by
> finding important problems that it is ideally suited to
> solve.
>
> E. O. Wilson (1986)

For as long as there have been men, they have been watching
animals. With mankind's increasing understanding and manipulation of
the environment, the way in which observing animals is of value has
changed. Once men were concerned with avoiding predators, and with
catching prey. Today our survival depends no less on our knowledge of
nature, but most people are removed from active pursuit of greater
understanding of the natural world, and those who do pursue it are far
more specialized.

The study of insect behavior is one such specialization. The
activities of insects are of vital interest to mankind, for the effects
of insects range from pollination of crops to transmission of diseases
deadly to humans. Moreover, the topic is of interest in increasing our
understanding of our own animalness, and of the behavior of animals in
general.

One aspect of animalness about which questions have been asked for
as long as there has been language is sex. Science, especially since
Darwin, has refined our concepts about sexual behavior. Darwin (1859)

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established the concept of evolution by natural selection. His successors, particularly in this century, clarified the mechanisms of adaptation and developed the powerful model of selection acting at the individual or gene level (see Dawkins 1976). New questions about mating systems were posed as a result of this conceptual revolution. The very definition of species became a question of who mates with whom. Observations of behavior (and other traits), previously colored by less powerful concepts, are now more productively considered in terms of how characteristics contribute to reproductive success (see Lloyd 1980 and refs.).

The studies presented here are concerned with production of the next generation by certain fireflies. At the time I began this project some of the recently posed questions in reproductive ecology had not been addressed by field biologists for lack of a suitable animal. I selected the firefly species Photinus collustrans Le Conte (1878) for study because it appeared likely to prove useful for investigations of some of these topics, particularly the subject of female multiple mating. Because many female insects obtain a lifetime supply of sperm with one mating, subsequent matings may not be required. Yet many female insects do mate repeatedly (Smith 1984 and refs.). My goal was to monitor females throughout their adult lives and document their complete sexual histories, in the field. This seemed an achievable goal with collustrans females because of their unusual lifestyle.

It was J.E. Lloyd who first explored the behavioral ecology of collustrans, exploited their accessibily, and guided his graduate students toward further study of the species. Lloyd's (1966) extensive survey of the fundamentals of behavior and ecology in the genus

illustrates the value of the accessible signal channel that most fireflies, including collustrans, share. Bioluminescent signals can be observed, recorded, and analyzed far more readily than chemical signals, for example (as Lloyd is fond of pointing out), and some are useful taxonomically (Lloyd 1966). But collustrans has additional attributes that make the species unusually valuable for field studies.

Members of many other firefly species are active at heights or in habitats that make them difficult, if not impossible, to observe at close range. But collustrans is a grassland species, and males usually fly between 0.5 and 1.5 m above the ground (Lloyd 1979b). Lloyd (1979b) utilized this combination of low-flying males over a grassland habitat by following nearly 200 individual collustrans males as they made signaling flights in search of mates. Lloyd was able to quantify distances travelled with a measuring wheel and record observations on tape during these chases. The resulting portrait of "a day--or rather evening--in the life" shows problems that males face and investments they make in the search for mates.

Another illustration of collustrans accessibility is provided by Adams' (1981, 1982) studies of male flight paths. Adams wanted to study search paths in 2 dimensions. Lloyd suggested collustrans as one subject of the study because males search at a relatively uniform height, and because it is possible to follow individual males. Also, the collustrans season is long, so much data can be collected in one year. As Adams followed individual males he dropped a marker under each flash. He graphed the paths described by these markers and ran computer analyses. The result was another notable contribution to field biology,

this one showing the changes in male searching strategy as the evening progresses.

Lloyd and Adams had taken advantage of the accessibility of searching males, but females remained relatively unstudied. Preliminary observations by Lloyd (1966, 1979b) and, later, Wing (1982) showed that females too have characteristics that make them accessible for certain observations.

Females are flightless and flash responses to flying males while stationed on blades of grass near the ground, or on the soil itself (Lloyd 1966). The open nature of the grassland habitat and the relatively exposed locations of responding females make them easy to find. Flash dialogues by which males locate females make pair-formation conspicuous.

As I found in a previous study of female movements (Wing 1982), females are not only easy to locate, but also easy to mark. They are pale, soft bodied, conspicuous, and relatively slow-moving. I found females by using standard lampyrological procedures, locating their flash responses to males or to male-like signals that I made with a penlight.

A female's signals give away her location, but to actually see a female I used a flashlight. I could then mark the pronotum or elytra with white ink. After replacing her on the spot where I found her, the female would soon resume her responses to flashes. (Similarly, mating pairs can be observed with light without seeming to disturb them.)

The results of marking were not entirely conclusive because the marking substance was not permanent in moist soil. However, the fact that collustrans females, like many other fireflies, can be manipulated

in such a way and will then resume their response behavior is another aspect that makes them good field biology subjects. But there is another characteristic of the species that is unusual and allows studies that could not be made on most other species.

As Lloyd (1966) noted, collustrans have a nightly mate-locating period of unusually brief duration (on the order of 18 minutes nightly for males). This means that it is relatively easy to monitor a female during the entire nightly period when she could attract a mate. By contrast, the nightly mate-locating period for some other firefly females may last eight hours or more (Wing 1985). But the whole nightly mate-seeking activity of a collustrans female may last half an hour or less. Not only is what a female does during the mate-locating period readily observable, but one is able to monitor her throughout the period. This is a key characteristic that allowed me to compile complete sexual histories of individual females (see mating frequency chapter).

Questions about what females do (i.e., how many times they mate) are not fully addressed without investigating why they behave in this way (see Thornhill and Alcock 1983). In considering this question, I examined two of the costs of mating, risk of predation and energetic costs. These costs also would be predicted to influence the timing of mating efforts (T.J. Walker 1983a), a study of which is also presented here.

In the Epilogue I suggest the beginnings of a way to organize comparisons of female firefly reproductive strategies. The accessibility of fireflies in general, as noted above, and the diversity within the family make such comparisons potentially among the most

instructive of any animal group. The studies presented here may prove
to have their greatest scientific value as a case for comparison. These
studies are also of value in that they address ideas about what may
occur in nature with evidence collected in the field. Such field
studies will contribute to formulating more accurate models of the
natural world, particularly regarding insect mating systems, and may
have unexpected value in other areas of biology (see Ballantyne 1987a,b
for an example of how understanding firefly mating was of major
significance in studies of the taxonomy of the group).

GENERAL METHODS AND MATERIALS

Methods and materials that were used in all of the subsequent chapters are presented here.

Field studies of Photinus collustrans were conducted at a site north of the Gainesville Regional Airport in Gainesville, Alachua County, Florida (NW 1/4 Section 24, TWP R20E, T9S). The site was a grassy field, mostly Axonopus affinis Chase (common carpetgrass), and Eremochloa ophiuroides (Munro) Hack (centipede grass). Most of the females were found on one section of the site under scattered trees (mostly Quercus spp., Pinus spp., and Myrica cerifera).[1] The remainder of the site was treeless. Two streetlights sometimes illuminated parts of the site. Females found in illuminated areas were not considered in timing studies.

I located females by their flash and/or glow responses to penlight simulations of male mating signals (see Lloyd 1966). The location of each female was marked by a numbered flag placed about 15 cm to the north of her. Flags were 10 x 40 cm strips of plastic held in place with nails. Females use the same burrow throughout their adult lives[2]

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[1] Lloyd (pers. comm.) has been observing fireflies at this site for over a decade, and most of the collustrans females that he has found were in the same restricted area where the females in this study were located.

[2] During this study 91 females were individually marked with Tech Pen Ink dispensed from Hamilton's paint pots (T.J. Walker and Wineriter 1981). Females appeared for up to 10 consecutive nights. Every appearance by each marked female occurred at her original position.

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(Wing 1982), and numbered flags were sufficient to identify each individual. Copulations were timed with a stopwatch, and some were observed with a magnifying glass.

To establish that individual animals contribute only one point to the data set (see Machlis et al. 1985) generally requires that they be identifiable as individuals. In these studies females were generally identified as individuals, males were not. Specific comments are included in the text.

FEMALE MATING FREQUENCY AND MALE COMPETITION
IN PHOTINUS COLLUSTRANS

Introduction

Although the consequences of multiple mating by female insects have
been discussed at length (Smith 1984 and refs.), few studies have been
published on female mating frequency in the field. This is partly
because such activities are difficult to monitor under field conditions.
However, as noted above, matings by Photinus collustrans females can
easily be monitored in the field. The brachypterous females live in
burrows and remain near them. About 20 min after sunset males start to
fly and search for females, which take positions on the soil surface or
on vegetation (Lloyd 1966). Females flash in response to the signals of
flying males, which locate females by their responses. Each night
sexual activity is restricted to a period about 18 min long (Lloyd 1966,
also see T. Walker 1983a for a discussion of such 'sprees'). Female
collustrans live about 10 days after their first appearance (Wing 1982);
by observing a female for about 20 min per night for 10 nights, every
sexual activity of her life can be recorded. There is no evidence that
females mate under circumstances other than those mentioned above and
some evidence that they do not (next chapter).

Methods and Materials

An 18 x 20 m area was searched for females nightly starting before
male flights began and ending after they had ended for the night. I

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marked the location of each female and I checked her position at approximately 1 min intervals.

Each time a female's position was visited on a given night, she was presented with penlight simulations of the male signal. Because females do not respond following a successful mating, but instead pause and then re-enter their burrow (Wing 1982), a female answer to my signal indicated that she was not yet mated. If she failed to respond, I determined whether she was (1) still at the burrow entrance but not responsive, (2) mating, (3) entering her burrow, or (4) gone. All female locations were checked until the adult season was over.

Because the same area was searched nightly throughout the season, when a new female appeared she was almost certainly a virgin making her first appearance. I recorded complete sexual histories of 108 collustrans females.

Results

Of the 108 females whose complete sexual histories were determined, 104 mated only once. The general sexual pattern was as follows. The female appeared by her burrow nightly until she attracted a male ($\bar{x} = 2$ nights). The male, having located the female by her continued responses to his signals, landed nearby and walked to her. Upon making physical contact, the male climbed upon the female and copulated with her in the male-above position (Fig. 1). Copulation lasted about 1 min (details below), and then the male broke the connection, dismounted, and flew away leaving the female outside her burrow. Following copulation the female paused for seconds or minutes, and did not flash responses to signals of passing males. She then entered her burrow.

Four females mated more than once. One of these females was dug from her burrow by a male, one was mated by a "sneaky" male, and two made themselves available to other males by their own behavior.

The two repeated matings due to female behavior occurred when females mated and entered their burrows, but on subsequent nights left their burrows, responded to male signals, and mated again. Only three of 108 females responded to signals on nights subsequent to the first mating. Two mated again of which one remated once, the other twice.

When more than one male landed at a responding female, the first male to reach her mounted and began copulation. The rival male attempted to mount the female (sometimes backwards, see Lloyd 1979b), and to break the pair apart (Fig. 2). As a result, the copulating male moved or was pushed off the female and the copulation proceeded in the tail-to-tail position, with variations. (In the tail-to-tail position the male and female face in opposite directions while maintaining genitalic connection (see Wojcik 1969). Due to disturbance by rival males, pairs were sometimes moved into odd positions, even with the female on the copulating male's dorsum.)

Copulations were significantly longer when rival males were present.[1] Mean duration for single male copulations was 57 sec (n = 23, range 30-185 sec) compared to 842 sec (n = 5, range 339-1410 sec) (Mann-Whitney (U = 115) P <.0005) (Zar 1974) when rivals were present (also see Rutowski and Alcock 1980). In these cases, copulating males maintained the genital connection until __after__ the females had entered

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[1]Males were not identified as individuals. However, intense competition for females among numerous males makes it unlikely that one male mated with more than one female (see Lloyd 1979b). Ideally, data would be paired for individual males each mating with and without other males present.

their burrow (Fig. 3). Females entered head first, dragging the coupled males backwards down the burrow. In one case, only the head and thorax of the male remained outside the burrow when genital connection was broken. After disengaging, males climbed out and flew away. After the mated male departed, in four of seven cases the rival male dug at the burrow opening (i.e., tried to remove the female from her burrow). Rival males located the burrow opening by antennating the soil. Rivals dug at the burrow (Fig. 4), sometimes completely entering it. On one occasion the male succeeded in removing the female from her burrow and mated with her (this accounted for the third multiple mating) (Fig. 5). Unsuccessful males dug for as long as 35 min before leaving. In some cases more than one rival male dug at the burrow (Fig. 6).

The fourth repeated mating resulted from another behavior of rival males and was observed once during this study and once since then. The rival "sneaky" male was non-aggressive, and made only occasional contact with the copulating pair. The rival gently antennated the pair and then walked away, returned and antennated the pair again. The copulating male stayed in the male-above position, and copulation was not prolonged. After copulation, the male dismounted and flew away, leaving the female outside her burrow. The rival male then located the female and mated with her.

Discussion

A large investment of search time is likely to be required for a male to find a responsive female (Lloyd 1979b). With a period of only about 18 min nightly in which to operate, the usual male strategy after

locating a female is to mate and, within a minute or so, return to the air searching for another female.

Females pause after mating but do not answer the flashes of passing males. They then enter their burrow. Fewer than 3% of the females that mated made themselves available to males again (also see Wiklund 1982). Whether or not remating by collustrans females is adaptive (see W.F. Walker 1980) is unclear.

During the pause before re-entering the burrow females are susceptible to another mating if found by another male. Even after re-entering the burrow a female may be dug up and remated. Generally, then, if a male can gain physical access to a female, he can mate with her. This fact has led to prolonged copulation when a rival male is present (see Parker 1970). Copulating males make the female physically unavailable by occupying her until she has returned to her burrow (see Sivinski 1983). Rival males try to break the coupled pair apart and attempt to gain access to the female by digging her from the burrow. The "sneaky" rival avoids triggering mate-guarding by the coupled male, and thereby gains access to the female after her first mate leaves.[2]

The complex of male strategies and counter-strategies shown here reflects how important the potential for female multiple mating can be, even when only a small proportion of females actually mate more than once. If the number of observed matings was increased enough, it seems likely that other strategies would be revealed, and exceptions to almost any of the usual behavioral patterns would be found.

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[2] It should also be noted that mated females are sometimes flooded from their burrows and may remate under these circumstances (Wing 1982 and unpublished).

Fig. 1. *Photinus collustrans* male (above) mounting female. Note burrow opening in background. The female is about 11 mm long.

Fig. 2. *Photinus collustrans* trio. Male on left is copulating. Rival has mounted female.
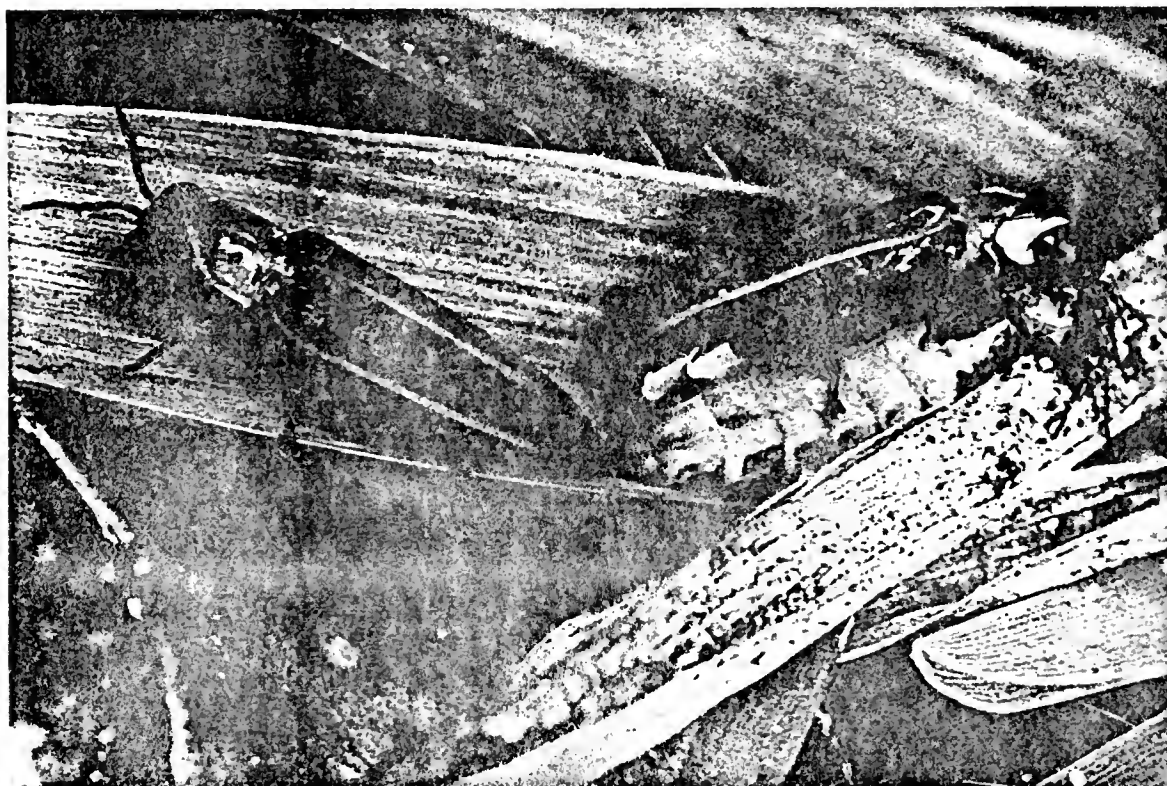
Fig. 3. Rival male (left) remains mounted as female enters burrow. Male on right is copulating.

Fig. 4. Rival male digs at female's burrow.
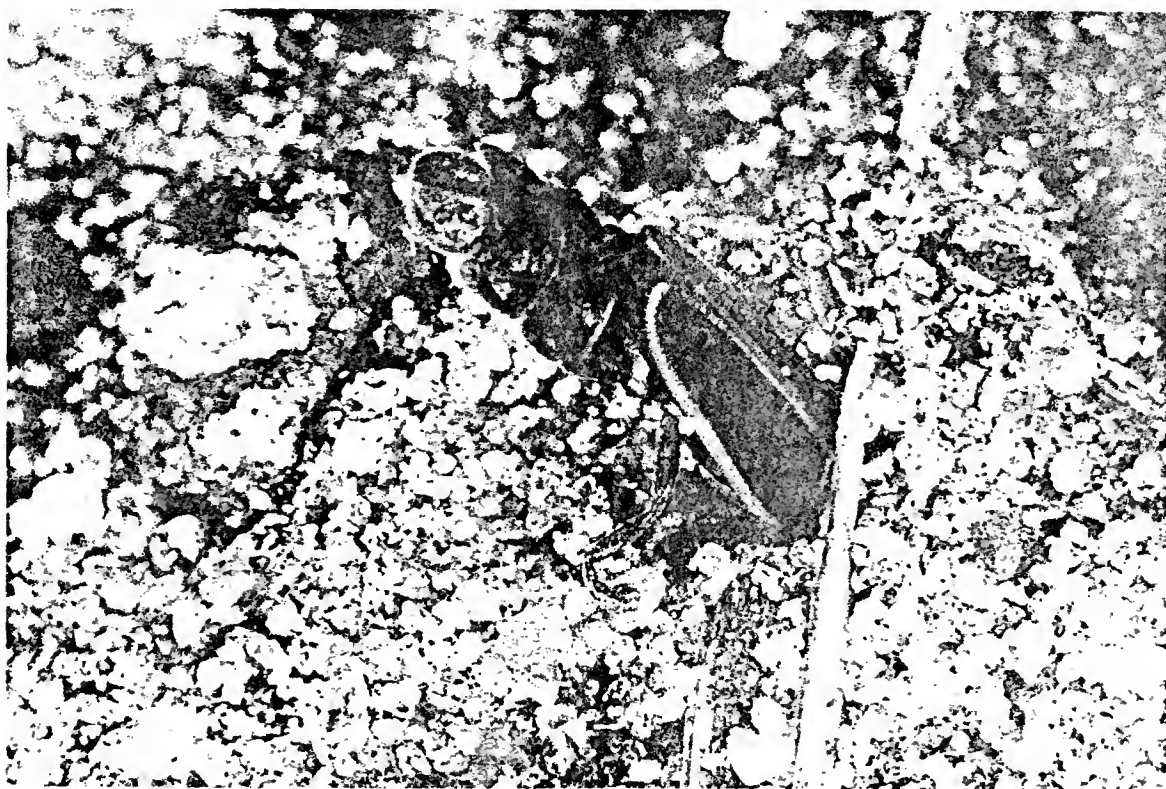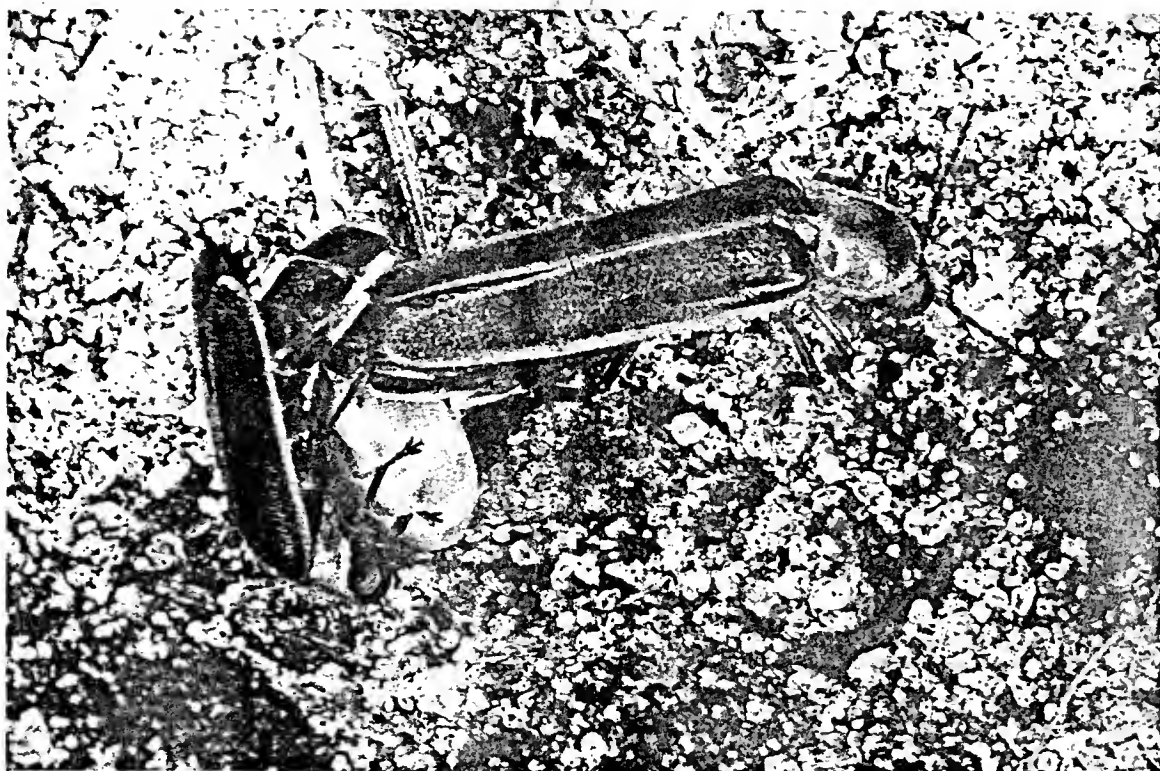
Fig. 5. Rival male pulls female from her burrow.
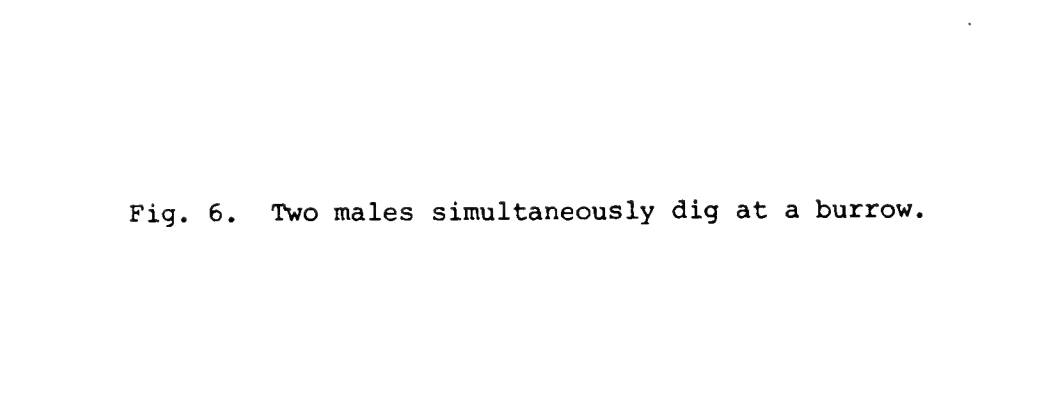
Fig. 6. Two males simultaneously dig at a burrow.
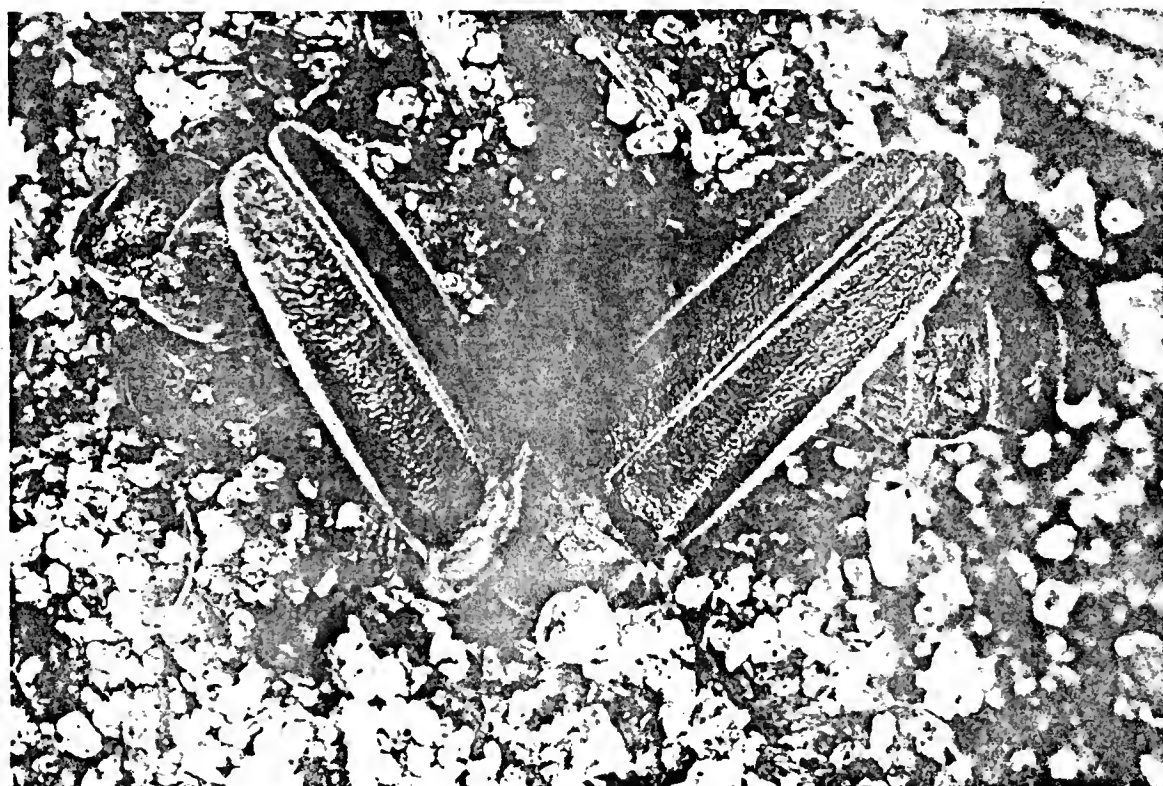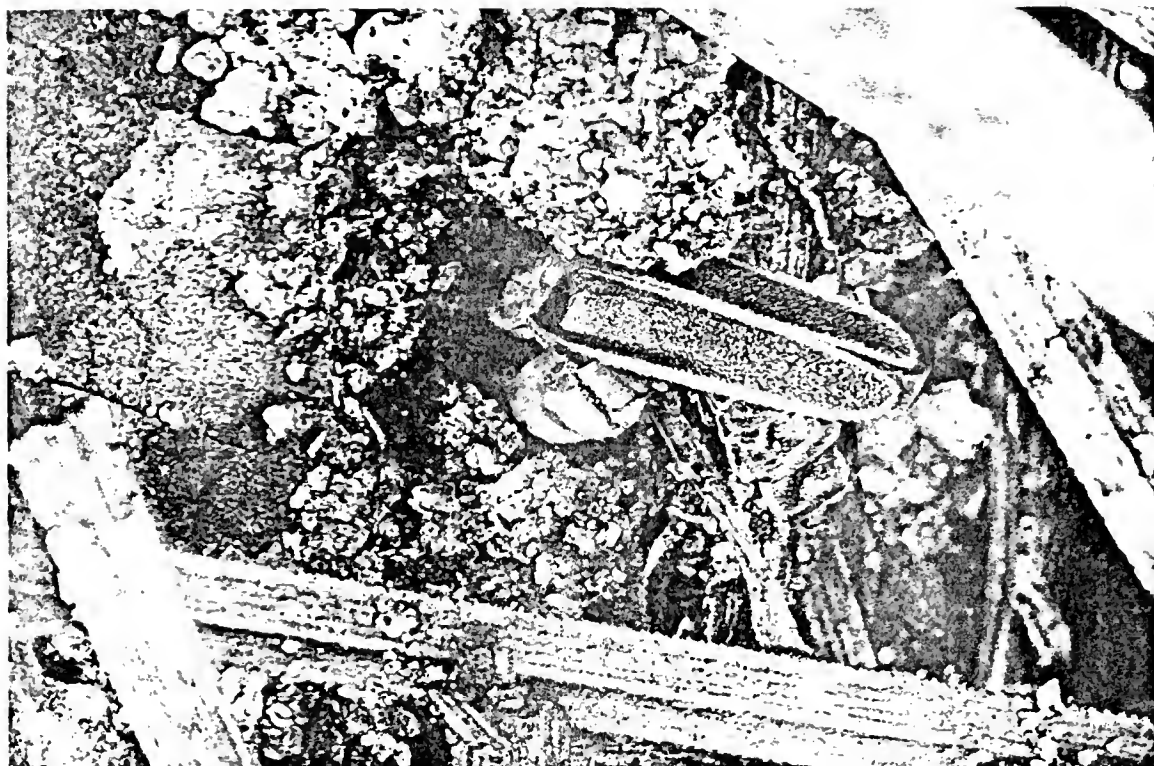
COST OF MATING FOR FEMALE INSECTS:
RISK OF PREDATION

Introduction

The cost of mating includes those expenses and dangers
". . . involved in locating mates, in courtship, in competition with
rival suitors, and in copulation . . ." (Daly 1978, p. 771). One of the
costs discussed by Daly is increased risk of predation associated with
mating. Such predation is expected to influence the evolution of mating
behavior (W.F. Walker 1980, Greenfield 1981, Burk 1982, T.J. Walker
1983a), and the concept of this mating cost is supported by examples of
predators that orient to the mating signals of male insects (Cade 1975,
Lloyd and Wing 1983). However, for females only circumstantial evidence
of this mating cost exists (Sakaluk and Belwood 1984; also see Verrell
1986a). In fact, better evidence suggests that some female insects are
actually protected from predators during mating (Sivinski 1983; also see
Verrell 1985a concerning males). This chapter provides the first
empirical evidence, for any animal species, that females experience an
increased risk of predation as a consequence of mating (see Sakaluk and
Cade 1983; Thornhill and Alcock 1983).

Assessment of this cost of mating for females has been hindered by
the difficulty of determining precisely when females are engaged in
mating activities. However, the reproductive behavior of a Photinus
collustrans firefly female can be unambiguously distinguished from

other biological activities. These females are flightless and inhabit burrows in the soil. A burrow is occupied by a solitary female, and she does not stray from the immediate vicinity of the burrow's opening (females do not move from one burrow to another, preceding chapter). During the brief period shortly after sunset when males signal, females take positions just outside of their burrows and flash responses to the signals of flying males. By flash dialogues males locate females and copulate with them (Lloyd 1966, 1979b). Daly (1978) suggested that such signals must disclose the locations of females to predators as well.

Mating costs are revealed by contrasting ". . . the costs incurred by a sexually reproducing female with those incurred by a hypothetical asexual reproducer" (Daly 1978, p. 771). Females of P. collustrans must leave the burrow to mate, thereby exposing themselves to predators found above ground. However, a hypothetical asexual female would not have to leave the burrow at all (below). The risk of predation associated with mating can be demonstrated, then, by showing that the risk of predation is greater outside of the burrow than in it.

Methods

To determine whether females leave their burrows at times other than during the male signaling period, I used two balsawood splinters (each with a black ring inked around its center). These were aligned to form crosshairs over the burrow opening. The crosshairs were disturbed in a telltale way by a female leaving (or entering) her burrow. Crosshairs were placed over the burrow after a female (of known mating history, methods explained in preceding chapter) retired for the evening. Data from 15 different females showed that, prior to mating,

females left the burrow only pursuant to mating, and mated females did not leave at all. The same was true of 14 females housed in vials with soil. These females appeared more or less nightly until mated, and thereafter stayed underground where they oviposited and died (Wing 1982). (A small percentage of mated females do return on subsequent nights for a second mating, preceding chapter.) Thus, crosshairs make it possible to detect the disappearance of a female, and to ascertain whether she was in or out of the burrow when she disappeared. Because females never leave the immediate vicinity of the burrow under normal circumstances[1] (preceding chapter; Wing 1982), disappearances can be safely attributed to predation.

Females spend most of the day in their burrows. Males fly during a period of about 18 minutes duration nightly (Lloyd 1966), and females usually stay out less than an hour (see chapter on timing). However, for convenience, the time spent outside the burrow by a female on one night was rounded up to one hour, and the daily time spent in the burrow was counted as 23 hours. (These figures err in favor of the null hypothesis, i.e., risk does not increase for the female outside of the burrow.)

Data were recorded as follows. When a female appeared, crosshairs were placed over the entry of her burrow. If the crosshairs were moved, indicating that the female re-entered, the hour was recorded as "safe." However, if she disappeared while out of the burrow (crosshairs not moved, indicating no re-entry) a lethal attack was presumed and the hour was recorded as "terminal." Also, when a known predator of these

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[1]Females may be forced from the burrow by flooding.

fireflies, a lycosid spider (Fig. 7, see Lloyd 1973), was seen attacking a female but apparently was frightened away by my light, a terminal hour was counted. (Predators suspected in the disappearances of other females included ants, a toad (see Lloyd 1979b), and reduviids.[2])

Mortality in the burrow was implied when a female known to be unmated failed to leave her crosshaired burrow on subsequent nights.[3] In such a case, 1 terminal hour was recorded. If instead the female did emerge the next evening, 23 safe hours were counted.

Results and Discussion

The results are shown in Table 1. Of the 944 hours monitored in the burrow, one hour was terminal. Outside of the burrow, 6 of 53 hours were terminal. The proportion of terminal hours in the burrow (1/944) was used to generate the number of terminal hours expected outside the burrow (1/944 x 53) if the risk of mortality does not increase.[4] A

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[2]The reduviid Repipta taurus frequently preys on collustrans males. In captivity one readily attacked a collustrans female. Photuris females also prey on collustrans males and are found on the ground at the site.

[3]One immature spider (Lycosa lenta) was found exiting from a female's burrow, but whether the tiny spider could prey on the much larger female is unknown.

[4]Females were monitored where they naturally occurred, scattered in space and time. Female collustrans are unlikely to vary much in ability to detect and avoid predators because females seem uniformly oblivious to other creatures (except flashing males) until physically disturbed, and they appear to be equally defenseless. The females I monitored were of similar ages and sizes, so presumably similarly attractive to predators. For these reasons I believe that the proportion of terminal hours in the burrow reflects the distribution and abilities of predators, giving a reasonable estimate of how often females in their burrows are found and attacked. However, the method of collecting data is not without risk. Females contributed more than one observation (i.e., hour) to the data set (23 hours for 1 safe night). This may constitute Pooling, and if so, statistical inferences based on the data could be jeopardized (Machlis et al. 1985).

Table 1. Comparison of safe vs. terminal hours spent by <u>collustrans</u> females in vs. out of the burrow.

| | Observed | | Expected | | |
	in	out	out	Z	P
Terminal	1	6	0.06	2.36	< .01
Safe	943	47	51.94	2.36	< .01

similar method was used to generate the expected number of safe hours outside the burrow. The one-tailed binomial test (Zar 1974) was used to compare the expected with the observed terminal and safe hours outside the burrow. For these females, the increase in mortality risk associated with being outside of the burrow for mating is statistically highly significant (P <.01).

Such increased risk is expected to influence the evolution of female mating behavior. When mating involves increased danger, females may minimize the time spent in courtship and/or copulation. In collustrans, this means minimizing the time spent outside of the burrow. Three aspects of their behavior may be involved. First, exits of females from their burrows coincide with the peak availability of males (see chapter on timing). Thus, females are outside when they have the best chance of being seen by a potential mate. Second, copulation durations of collustrans pairs are remarkably brief by known firefly standards (see Epilogue). Other fireflies, with more vagile females, may couple for hours or days, but usually collustrans matings last about 1 minute (preceding chapter; Wing 1985). Third, although females of other firefly species are known to mate repeatedly[5] (Wing 1985; Sara Lewis, unpublished), collustrans females generally copulate only once (preceding chapter). As a result of these 3 characteristics, a collustrans female may leave the burrow only once in her adult life and return to the burrow within a few minutes carrying her store of sperm. More extreme still, subterranean females of at least one other firefly

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[5]Females have never been observed to plug the entrance to the burrow even after mating. This is compatible with the notion of relative safety in the burrow, although it does not necessarily support the idea because the burrow may be left unplugged for other reasons.

species, _Lucidota luteicollis_, may completely avoid coming above ground for mating. These females sometimes mate through the sand, apparently attracting their aboveground males with pheromones instead of light emissions (Warren Prince, unpublished; Lloyd, unpublished). This signaling channel may have evolved in lampyrids in response to predation (see Greenfield 1981). Of course, many other factors may also influence the evolution of reproductive characteristics such as these (Thornhill and Alcock 1983).

Fig. 7. A spider with its prey--a _collustrans_ male captured on the ground. This male seemed to mimic female responses to flying males, as Lloyd (1973) observed a captured _Photuris congener_ male to do.
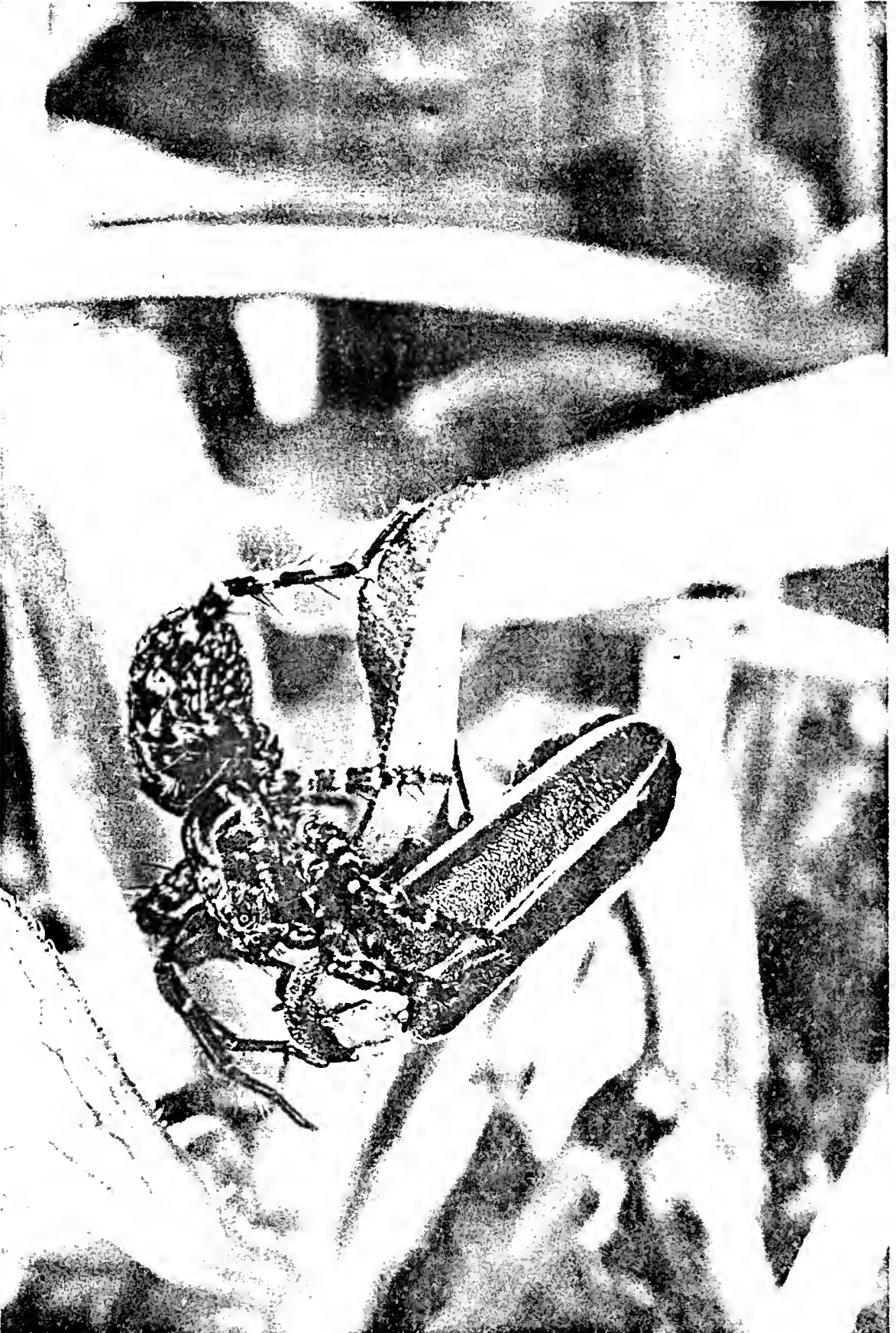
ENERGETIC COSTS OF MATING

All cold blooded animals . . . spend an
unexpectedly large proportion of their
time doing nothing at all, or at any
rate, nothing in particular.
                    Charles Elton (1936)

Introduction

Daly (1978) noted that there are energetic costs of mating.

"Besides the costs of producing structures (including behavioral

substrates), the actual performance of behavior costs time and energy

too" (also see Verrell 1985b). Female collustrans invest some of their

resources in mating-related structures, including compound eyes and a

sperm storage organ, and invest time and energy in excursions above

ground in the quest for a supply of sperm. Hypothetical asexual

fireflies could avoid these energetic costs of mating, remain in the

soil, and deposit their eggs without delay. The focus of this chapter

is the cost of delaying oviposition to accommodate acquisition of sperm.

The acquisition of nutritional substances by an animal is an

important component of energetic costs of mating. For example, some

female insects acquire substantial nutritional resources as a result of

mating. Some scorpionfly males capture prey which are presented to

females during courtship, and on which females feed while mating

(Thornhill 1980). In many Orthoptera, spermatophores of considerable

food value are passed to females, which eat them (Gwynne 1980). In

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other insects, the spermatophore is apparently digested within the reproductive tract (Boggs and Gilbert 1979). In these cases, sexual females could produce more eggs than hypothetical asexual females that did not enjoy the nutritional benefits of mating. However, collustrans females seem to be at the other extreme. They are among the least likely fireflies to gain nutritionally from mating, judging from comparisons of firefly male accessory glands and mating durations (Wing 1982, 1985), lack of female multiple mating, and the fact that no nuptial feeding has been observed (see Epilogue).

Furthermore, I have tentatively concluded that collustrans females do very little, if any, feeding as adults. In observations of hundreds of females out of their burrow for mating, I have seen no feeding, and there is evidence that females do not feed while in the burrow either. Larvae that eclosed from eggs deposited in "ant farm" burrows by mated females survived for as long as a year by actively hunting and feeding on small earthworms (Fig. 8) in the soil. However, females remained stationary while in the burrow, and did not hunt prey underground. Unmated females remained facing the burrow entrance, rarely moving except to leave in the evening and to return. Mated females moved around in the burrow depositing eggs, and shortly thereafter died (Fig. 9).

Female collustrans, then, apparently enter adulthood with certain metabolic resources which they do not replenish. A delay in oviposition to accommodate mating must be financed from these resources, which should result in the production of fewer (and/or perhaps smaller or lighter) eggs (Yuma 1984, Forrest 1986, Karlsson 1987). This study considers effect of delayed mating on egg count.

Materials and Methods

Mated and unmated <u>collustrans</u> females were collected in the field
and housed in the laboratory. Some were kept in cylindrical plastic
vials (3 cm diam x 2½ cm deep, with lids) with soil from the site.
Others were housed in plexiglass-sided sandwiches similar to "ant
farms." These were constructed from 2 plexiglass panes spaced 6.4 mm
(¼") apart with a U-shaped plywood frame. Through the top opening the
"farm" was filled about 3/4 full of soil from the site. A ∿ 3 cm deep
burrow-like impression in the soil was made so that one wall of the
burrow was plexiglass. On each side of the burrow a deeper impression
was made for adding distilled water with an eyedropper. A removable
plywood crossbar blocked the top. Cardboard covers were clipped in
place over the outside of the plexiglass except during daily
observations, some of which were made with a dissecting microscope.

The weight of some females was followed over time by weighing
them periodically on a Mettler digital balance accurate to .001 g. For
weighing, live females were cleaned under a dissecting microscope by
gently brushing off soil grains.

Some females of known weight were dissected and counts of eggs were
made. A computerized statistical analysis program, SAS Proc GLM, was
employed to analyze the relationship between female weight and number of
mature eggs.

Other females were left undisturbed in the field and observed
nightly. The locations of these females were marked with numbered
stakes, so that individuals could be identified and monitored over time.
Females that had not succeeded in mating for several nights were

collected and dissected for egg counts, to compare with counts from females collected on the first night they appeared.

Results and Discussion

On their first night (Fig. 10), females contained $\bar{x}$ = 71 eggs, n = 15 females, range 30 to 112 eggs, SD = 23. But females that continued mating efforts, without success, for over a week were almost devoid of eggs and grew very thin (Fig. 11).[1] Two females were dissected, one after attempting to mate on 7 consecutive nights, the other 10 nights. They contained 10 and 9 eggs, respectively. Based on these data, females seem to lose an average of about 7 eggs per day.

In the laboratory, egg "loss" was followed by weighing females periodically. The validity of this approach was shown by correlation and regression on number eggs vs. weight. Based on the "wet" weights of 15 females of various ages that were subsequently dissected for counts of full-sized eggs, there was a correlation coefficient of .93 for egg count vs. weight. A regression on these data shows that the number of eggs = .78 x weight in mg (F = 76.41, Pr $>$ F .0001, R^2 = .86 (Fig. 12).

Four females weighed periodically lost weight (and therefore eggs) consistently over time (Fig. 13). Again, an average loss of several eggs per day is indicated, although the rate of loss may change. These unmated females did not deposit eggs in their vials, suggesting that the eggs were metabolized to fuel continued mating efforts.

Entering adulthood with non-replenishable metabolic resources has implications for how the reserves are used in the ultimate mission of

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[1]Such females glow less brightly than younger females, which probably makes them less conspicuous to males. (See Schwalb 1961 for a case of aging females that glow more brightly.)

the female, egg production (see Fritz et al. 1982). Female collustrans are among the more semelparous of fireflies (see Epilogue). When they first appear, most collustrans females already have nearly all their oocytes fully developed. Mated collustrans females housed in "ant farms" deposited their eggs in the walls of the burrow over a period of few days, and then died in the burrow.

The strong correlation of eggs and weight is another indication of the semelparous extreme exhibited by collustrans females. Females that ripen several clutches of eggs over time, such as some Photuris species apparently do, would not be predicted to exhibit such a strong correlation, especially if they periodically acquire nutritional substances (e.g., prey). In this case a female's weight and egg count could fluctuate through adulthood. A heavy female that had just acquired a nutritional supply, but had not yet matured a clutch of eggs, for example, could contain the same number of mature eggs as a female with an empty stomach that had just oviposited and weighed much less. But first night collustrans females carry their entire and only clutch of eggs, and the longer the delay before oviposition the fewer eggs are left to deposit.

Unlike the risk of predation, which is a possibility for these females that are exposed during mating efforts, the loss of eggs in prolonged efforts to mate is an inevitability, a certainty. Staying in the burrow except for mating not only affords protection from predators, but also conserves energy. The possible effects of the costs of mating on the timing of female mating efforts will be discussed in the next chapter.

Fig. 8. First instar _Photinus collustrans_ larvae feeding on an earthworm "underground."
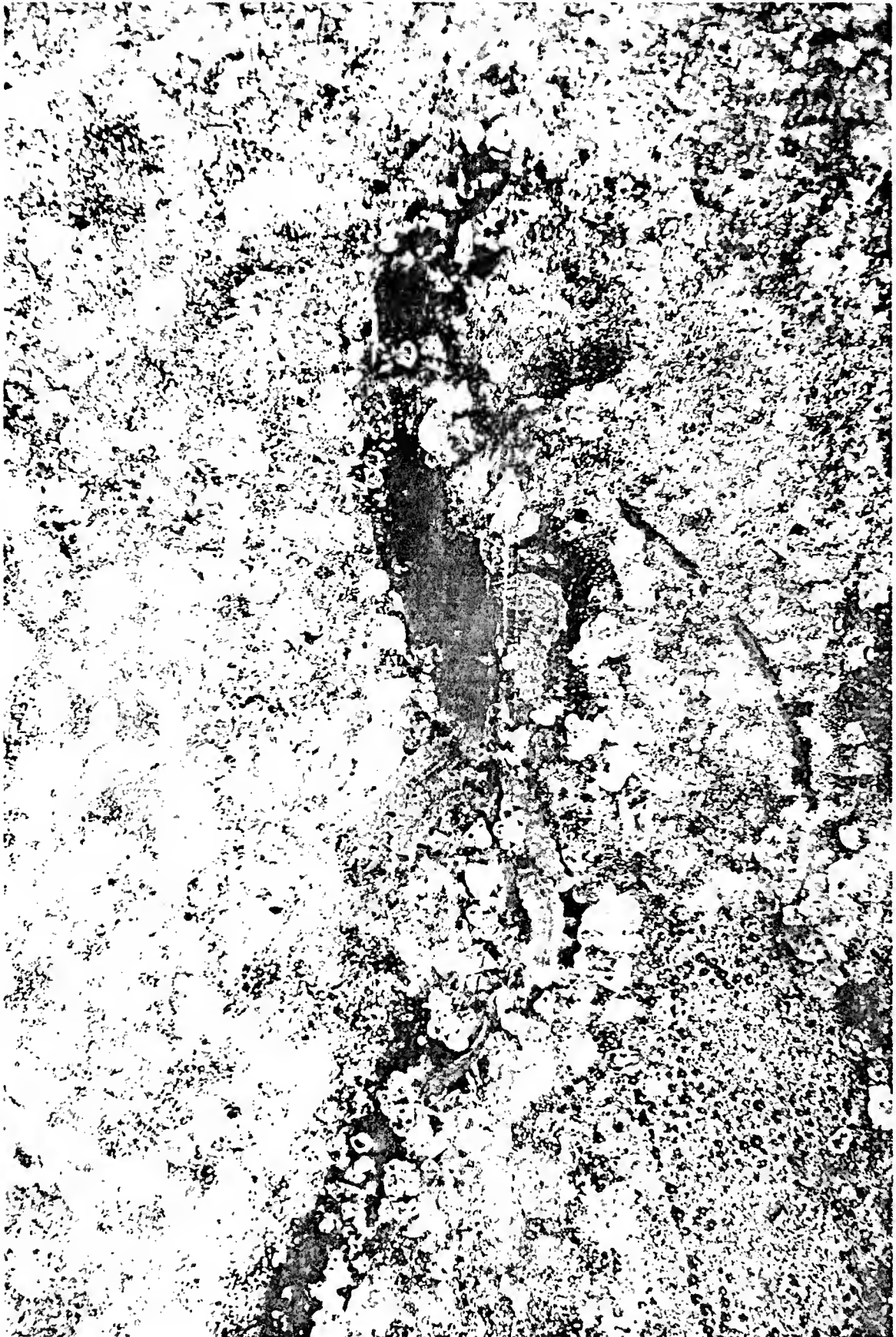
Fig. 9. *Photinus collustrans* female in her burrow in the laboratory. Note eggs in the soil below female.

Fig. 10. Typical _Photinus collustrans_ female on the night she first appeared.

Fig. 11. _Photinus collustrans_ female on the 9th consecutive night. On the night she first appeared this female looked like the female in Fig. 10.
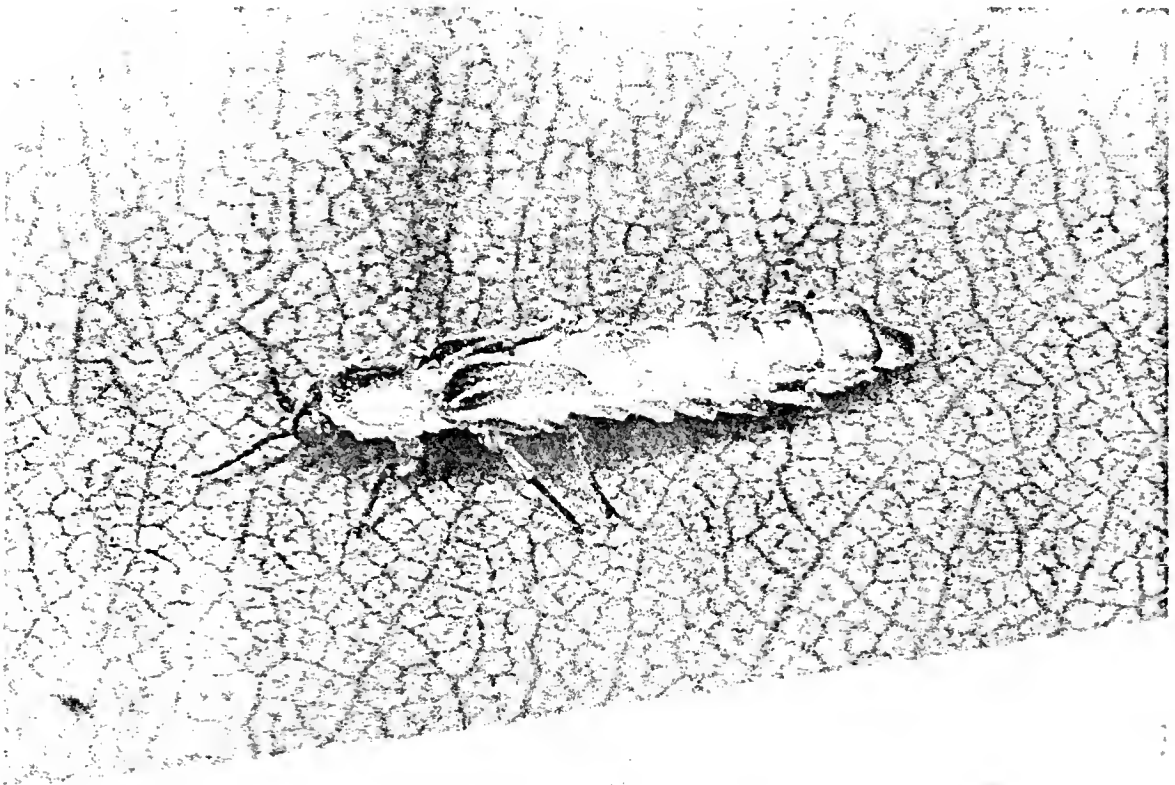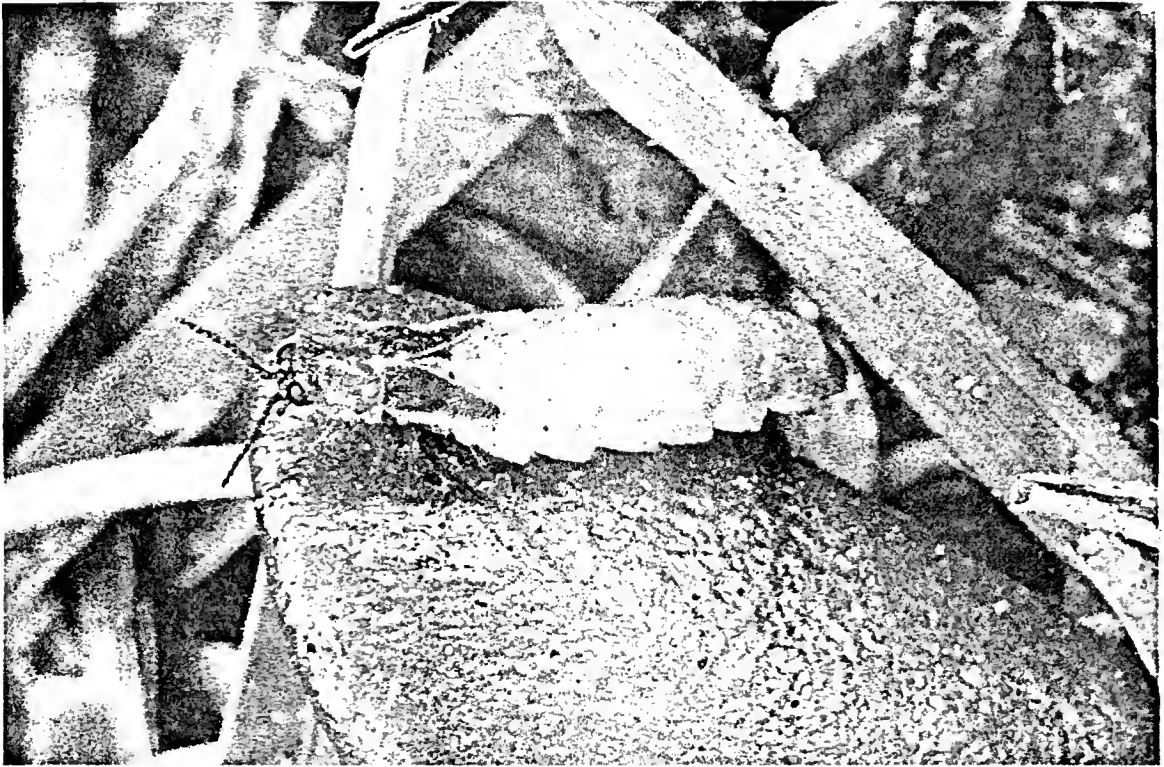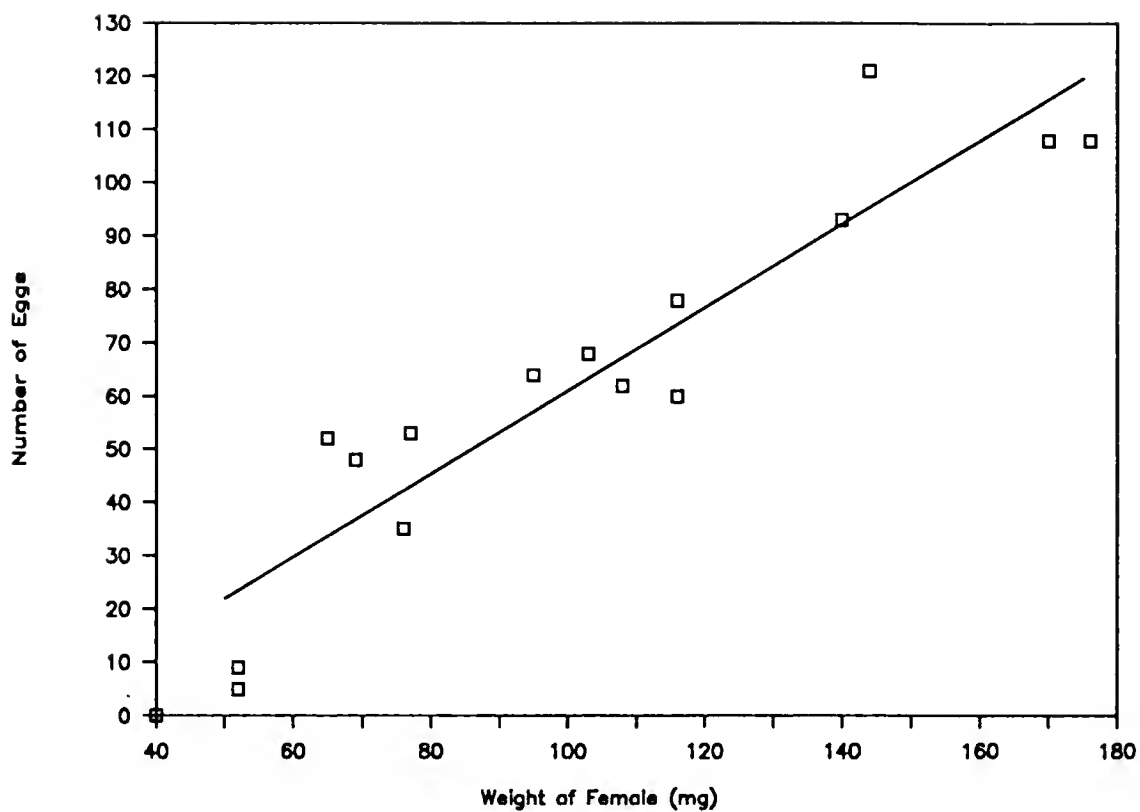
Fig. 12. The relationship between the weight of a female and the number of mature eggs she carries.
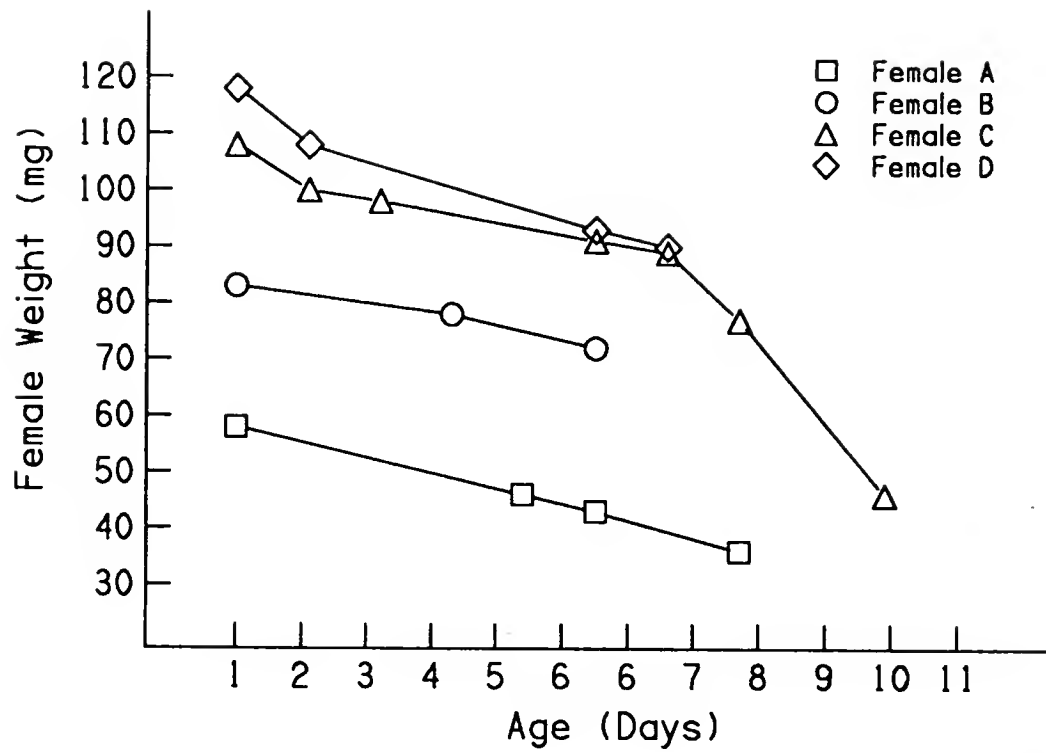
Fig. 13. Changes in the weights of four females over time.

TIMING OF REPRODUCTIVE ACTIVITY:
FINDING A MATE IN TIME

Introduction

Absolute failure to reproduce can be avoided, in most sexual
insects, only if a male and a female find each other in time and space
and mate.[1] This chapter is concerned with the temporal locating of
mates by Photinus collustrans adults. Two components of finding a mate
in time will be discussed. First males and females must synchronize
their adulthood, so that reproductive maturity occurs simultaneously in
the two sexes (seasonal synchrony). Second, males and females must be
sexually active at the same time of day (diel synchrony).

Methods and Materials

Field studies of collustrans were conducted during the years 1982
through 1985.

Males

Maturity periods were determined during nightly visits to the site
from April to October during the years 1982 through 1984. During 1985
weekly visits were made. The presence of collustrans adults was
detected by their flashes. The start of male activity was recorded as

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[1]In some apterygote species, sperm transfer can be accomplished without
the meeting of male and female. Males deposit spermatophores on
substrates where females later encounter these sperm packets and become
inseminated in the absence of males (Schaller 1971; also see Turk 1988).

the time when the first male of the evening was seen flying and flashing under the trees where females were most numerous. The last such flashes ended the male activity period. The duration of the activity period was thus the time between these first and last male signals.

An index of male abundance was obtained by counting the number of signaling males crossing a transect during the activity period. This was done approximately once a week during 1983 and 1984.

In 1983, the nightly timing of male abundance was determined as follows. The time of the first male signaling flight under the trees was noted. At the beginning of the next minute, I started a stopwatch and began counting the flashing males crossing a 15.2 m (50 ft) transect between two of the trees. The same transect was used all year.[2] The males that crossed the transect were counted on a hand-held mechanical counter. The running count and the number of minutes that elapsed since the appearance of the first male were recorded at the end of each minute. The transect was watched for at least two minutes after the last male flew across the transect, by which time there were no signaling males flying in the area (under the trees). The number of males crossing the transect during each minute after that evening's sunset was calculated. These data were summed over the season to produce a graph of the timing of male abundance in terms of number of males crossing per minute after sunset.

The study of the timing of male abundance was repeated in 1984 with the sample unit being instead the number of males crossing per 1/25 crep (Nielsen 1961) rather than minutes after sunset. Crep is defined by

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[2]Male activity occurs in the same area throughout the season.

Nielsen as the duration of civil twilight[3] in minutes. The crep value is 0 at sunset, and 1 at the end of twilight. Crep values were used to correct for differing rates of the onset of darkness over the season, and to make the results of this study comparable to similar studies at other altitudes and/or latitudes, and/or seasons. In the 1984 study the same methods and materials were used as in 1983 except that the stopwatch was replaced with a programmable timer. The timer was programmed to beep at intervals of 1/25 of whatever the crep unit for that evening was. (The crep unit varied from 23 to 28 minutes over the season.) The running count of the signaling males crossing a 6.1 m (20 ft) transect (the northern 2/5 of the 1983 transect) was recorded at intervals of 1/25 crep. The data for the 1984 season were summed over the season to produce a frequency distribution of male activity in terms of crep units.

Although the 1983 male data collected in minutes after sunset, discussed above, cannot be converted to crep units as accurately as data on females (below), an approximation of the frequency distribution in creps was produced as follows. The average of the duration of twilight in minutes for the evenings on which males were counted was calculated (= 26 min). The summed data of number of males crossing per minute after sunset in 1983 were converted to number crossing per 1/25 crep (= 1.04 min) by multiplying the fraction of the minute after sunset overlapping a particular 1/25 crep by the summed number of males counted in that minute. Adding together these numbers of males corresponding to each 1/25 crep gave a total number of males crossing per 1/25 crep.

[3]Civil twilight is the time between sunset and when the center of the sun is 6° below the horizon.

The 1983 male data converted to approximate the temporal distribution in crep units (above), and the 1984 data which were recorded in crep units were combined to produce a generalized curve for males as follows. To give each year equal weight, although 7.26 times as many males were counted in 1983 as in 1984, each 1983 count was multiplied by 1/7.26. The resulting 1983 counts were then added to the 1984 counts. These combined counts were used to calculate the more meaningful percent of total males crossing.

Females

Data on female seasonal (annual) abundance and the timing of their availability were collected during the 1982 and 1983 seasons.

An 18 x 40 m area was searched for females nightly starting before male flights began and ending after they had stopped for the night. The location of each female was marked and I inspected her position at approximately 1-min intervals (these inspections are elaborated on in the Methods section of the chapter on mating frequency). Complete histories of the sexual activities of individual females were accumulated. This provided data concerning seasonal abundance and the daily timing of the sexual availability of females of known 'ages.' On the night of her first appearance a female's age was 1 night. If she appeared the next night, her age was 2 nights, and so on. (Note that I have not determined when, in relation to eclosion as adults, females make their first appearances to answer males.) The nightly timing of availability was summed over the season in temporal units of minutes after sunset for comparison with the 1983 data on number of males available in minutes after sunset. The data on female availability were

also converted to crep units for comparison with the combined 1983 and 1984 data on males available per 1/25 crep.

Because males were scarce in 1982, the timing of female availability was studied again in 1983, a year when males were abundant. Because the search for females could not be made every night (as it had been in 1982) due to the weekly transect counts of males, the female data were treated as follows. For data concerned with female age, a female was assumed to be making its first appearance as an adult (age = 1 night) only if she was a female that had not appeared the previous night and that looked young (the abdomen appeared plump and white, Fig. 10). Females that were first found on the night following a count of males were considered new, but age (and mating history) unknown, and these were excluded from analysis that required age values.

The relationship between the number of males counted crossing a 20-ft transect on a given night to the number of males that a female might see was investigated (also see Otte and Smiley 1977). In order to determine whether a female positioned on a transect could see the flash of a male flying ten feet down the transect, the following was done. A collustrans female in the field was presented with flashes from a very dim penlight (these appeared to my eye dimmer than male flashes). While making these flashes I stood ten feet away from the female (as measured on the ground) and held the penlight about 1½ m above the ground. This was repeated on 3 other sides (∿90° apart) of the female.

The response of females to the flashes of males of different species was tested by presenting females with flash patterns of various species made with a dim penlight. These tests were done when there were no collustrans males around for the females to respond to.

Results and Discussion

Seasonal Abundance

Adult collustrans were found during the warmer half of the year. The first adults were found in mid-April, and the last in late September or early October (Fig. 14a-e; also see Lloyd 1966 and Adams 1982).

All other things being equal, the more males there are searching for females, the fewer females will be found in the nightly sample. This is because females are located by their flash responses, and they cease to respond once mounted by a male (Wing 1982). This fact complicates comparisons of absolute numbers of females found during times of different levels of male abundance. Nevertheless, three patterns in annual (seasonal) abundance are clear.

Bimodal population peak

First, there are two annual abundance peaks (as Lloyd's unpublished census data recorded over the last two decades also indicate, pers. comm.). This pattern is evident for both males (Fig. 14b,e; 1983) and females (1982 and 1983; Fig. 14a,b,e). There is a peak in late April and early May, and another from August to early September. During the time between these peaks the population of adults sometimes drops to zero (1981, not shown). However, the 1984 and 1985 data (Fig. 14c,d) show that there are not always two annual peaks.

Fluctuating abundance

The second pattern evident from the data in Fig. 14 is large annual fluctuations in population size. There was a severe drop in abundance beginning in the summer of 1984 (Fig. 14c,d) and lasting at least through 1987. Males were virtually absent at the site for most of 1985. The total counted over the season was less than the number of males that

crossed a 20-ft transect on some individual nights in 1984. Similarly, in 1982 over 300 females were found by searching one 18 x 20 m area nightly. During 1985 (not shown in Fig. 14) only 21 females were found during 27 weekly extensive searches of the entire locale, with almost no competition from searching males.

The rainfall pattern probably contributed to this decline (also, see Yuma and Ono 1985). Because collustrans females and immatures inhabit the soil, they seem to be sensitive to both flooding and to drought. Flooding left standing water on the female search area for weeks during the summer of 1984, and no summer abundance peak occurred. During such floods bioluminescent, soil-dwelling creatures including collustrans females, Photinus spp. larvae, and phengodids (Wing 1984) were found dead on the surface of the water or clinging to vegetation.

Following the 1984 summer flood, a drought occurred. Larvae are presumably developing between October and March in North Florida (voltinism is unknown). During this study ∿ 20 inches of rain fell before the 1983 adult season (recorded about 1.1 km from the site by the Federal Aviation Authority), and ∿ 21 inches fell before the 1984 season. However, only ∿ 8 inches of rain fell before the 1985 season, and very few adults appeared. A similar drought preceded the 1981 season, when adults were also scarce (not shown).

Corresponding male and female peaks

The third pattern evident from Fig. 14 is that in both 1983 and 1984 (Fig. 14b,c) peaks of male and female abundance are more or less synchronized. Males and females are most numerous during the same weeks of the year.

Finding a mate in seasonal time is a developmental problem. An insect must reach adulthood with members of the opposite sex. Immature members of both sexes share the same habitat through the larval and pupal stages. Thus, each has the same information (cues) available with which to time its eclosion. As discussed below, once they become adults, males and females no longer have identical access to timing cues.

One final point regarding Fig. 14: the 1984 male data (Fig. 14c) give a conservative estimation of the number of males a female would see in a night if she were out for the entire male activity period (i.e., a range of 0 to over 200 males per night). This was shown by testing whether females could see (would respond to) male-like flashes 10 ft down a transect. Of 5 females tested, all consistently responded to signals produced on at least 2 sides.[4] This indicates that a female could see all the males crossing a 20-ft transect (as was used in 1984) if she were positioned in the center. (See Lloyd 1979b for similar data on males; also see Otte and Smiley 1977.) Changes in male density, such as those shown for the 1984 season, can influence the time required for a female to get mated (see Dreisig 1971 and Lloyd 1979b).

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[4]As noted by other researchers (Forrest, pers. comm.; Lloyd, pers. comm.; Sivinski, pers. comm.) females can often see a flash much farther away than 10 ft. One of the females tested responded to flashes I made while standing 25 ft away. Definitive research on the female field of vision was beyond the scope of this study. A female should be observed during testing to determine whether she changes position, but such observation should not interfere with her ability to see the male-like signals. I was unable to do this with my rudimentary equipment. In the tests reported here, which were done in the field, obstacles such as grass could have prevented females from seeing the signals at some angles.

Timing of Nightly Sexual Activity

In collustrans, and perhaps most other species of luminescent

fireflies, it is the males that actively seek mates by making signaling

flights (Lloyd 1966, 1971; also see Greenfield 1981 and Burk 1982).

Female collustrans make themselves available by exiting from their

burrows, perching nearby, and responding to male signals (Lloyd 1966,

1979b; Wing 1982). What is unusual about the temporal ecology of

collustrans is the brevity of the nightly period during which

mate-locating occurs. Males of some other firefly species, for example

Photinus macdermotti, make signaling flights throughout the night (Wing

1985). The duration of the collustrans male activity period is one of

the briefest known, being limited to about 18 minutes nightly (Lloyd

1966). For collustrans females, it is critical to be available during

this same 1% of the (24 hour) day that males are active. This section

is concerned with how females achieve the temporal overlap with active

males. First, some details of the timing of male activity are examined.

The timing of female availability is then explored, and compared with

the timing of male mate-locating activity.

Timing of male activity

In this study the male activity period is defined as the time

between the first and last male signaling flight of the evening. The

period occurs soon after sunset, a time when the ambient light level is

rapidly changing (see Dreisig 1971). That ambient light is the cue that

male fireflies use to determine when to make signaling flights has long

been recognized (see Lloyd 1966; Dreisig 1974). Males in darker

(forested) habitats begin signaling flights before males in lighter

(open) habitats do (Lloyd, pers. comm.; Sivinski, pers. comm.; also, see

Dreisig 1974). In this study the males under the trees always started before males in the adjacent pasture (sign test, n = 24 nights, P < .0002).[5] The nonparametric sign test utilizes only the direction, or sign, of the difference between members of a paired sample (Zar 1974). In this case the paired sample is the start time of males over the pasture and the start time under the trees on a given night. If males start first over the pasture, a + is arbitrarily assigned, and if they start first under the trees a -. The sign test is used to determine the probability of the observed distribution of + and - if the null hypothesis is true. The null hypothesis is that males start over the pasture at the same time as those under the trees (sign = 0), or the frequency of positive differences is equal to that of negative differences. Males under the trees also stopped before males over the adjacent pasture (sign test, n = 15 nights, P < .001). Another indication of male reliance on ambient light cues is their earlier activity when the western sky is darkened by clouds (see below).

In any one habitat, e.g., under the trees, male activity might be expected to start and stop at about the same time each night, and the duration of activity should be constant from night to night. However, there is variation in the timing of male activity. In 1983 durations ranged from 9 minutes to 26 minutes (n = 57 nights, mean = 16 min, SD = 3 min) (also see Lloyd 1966). Such variability can be due to variation in starting time, stopping time, or both. Starting time is considered here first.

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[5] An indivudual male could have contributed more than one point to the data set, either by being the first male in both areas within a night, or by being a first male on more than one night. However, the probability of either is slight owing to the large number of males.

In 1983 male start times (n = 72 nights) ranged from 9 to 22 MAS (Minutes After Sunset) with a mean male start time of 15 MAS (SD = 3.5 MAS). Variation in male start time is partly accounted for by external factors that influence the time at which the critical ambient light level occurs. Two of these factors are cloud cover and time of year (how fast the light fades after sunset) (Table 2).

However, the major source of variation in 1982 male start times was apparently not abiotic, but biotic in nature. Start times within the season occurred earlier when the density of searching males was high (Table 2) (also see Lloyd 1966).

The cause of this correlation remains unclear. There is probably some variation among individual males in what level of light triggers signaling flight behavior (see Dreisig 1971). In a larger sample one might expect to find more "outliers" and an earlier first male. An alternative explanation is that males are observant of and influenced by the behavior of other males (see Lloyd 1979, 1982). Adams (1981) quantified differences in collustrans males' flight patterns depending on male density. Thus, there is evidence that collustrans males do observe other flashing males and modify their behavior accordingly.

The variation in male stop times was also analyzed by regression (Table 3). The factors that make darkness come earlier, shorter crep and increasing cloud cover, resulted in males stopping earlier (although the significance level of clouds is marginal at n = 20). However, the effect of male density (transect counts) on stop time was not significant (Table 3).

In considering variation in duration, the effect of clouds cancels itself out. When darkness falls earlier, males start earlier (Table 2),

Table 2. Sources of variation in male start times.

Variable	F value	Prob. > F	
number	20.72	.0003	
crep	5.73	.03	
clouds	4.63	.05	Rsquare = 0.71

Slopes:
  number   -0.01 (Start ∿1 min earlier per additional 100 males.)
  crep   0.95 (Start 57 sec later per min added to crep.)
  clouds   -3.62 (Start almost 4 min earlier if clouds 100% as
                 compared to 0%.)

Regression on dependent variable start time. Significance level for entry into the model = 0.15. Model: start time = number * crep * clouds. Number observations = 20 nights. The variable "number" = total number of males crossing the transect that night. "Clouds" = estimated % of western sky occluded. (Proc. Stepwise, SAS 1982.) "Crep" is number of minutes in 1 crep.

Table 3. Sources of variation in <u>collustrans</u> male stop time.

Variable	F value	Prob. >F	
crep	3.77	0.044	
clouds	2.91	0.106	Rsquare = 0.31

Number did not meet 0.15 significance level for entry into the model.

Slopes:
   crep   0.88 (Stop ∿53 sec later per min added to crep.)
   clouds -3.28 (Stop over 3 min earlier if clouds 100% as
                       compared to 0%.)

Regression on stop time. Significance level for entry into the model = 0.15. Model: stop time = number * crep * clouds. n = 20 nights. (Proc. Stepwise, SAS 1982.) "Crep" is the number of minutes in 1 crep.

but they also stop earlier (Table 3), so that duration is not

significantly affected. Nor was the effect of crep on duration

significant. The major factor accounting for variation in duration was

male density (Table 4, Fig. 15). As shown above, the number of males

affects duration by affecting start time, not stop time.

The data above provide a measure of what time of day ANY males are

making signaling flights. This section shows how, within that time

period, the numbers of active males are distributed. The minute-by-

minute counts of males crossing the transect (made more or less weekly,

n = 24 counts) were summed over the 1983 season to produce Fig. 16.

Note that the graph shows the number of active males counted per minute

after sunset (MAS). As also noted by Lloyd (1966, 1979b) and Adams

(1981), the pattern shown in Fig. 16 is the same as that observed on

individual nights: male activity rapidly plateaus and then ends

abruptly.

Similar data were collected in 1984, but in crep units rather than

in MAS. For comparison, the data in Fig. 16 were used to approximate

the temporal distribution of 1983 males in crep units. Data from both

sources were used to produce Fig. 17. The comparison shows that the

distribution is fundamentally the same from one year to the next. These

data were equally weighted and combined to produce Fig. 18. These

frequency distributions (Figs. 16 and 18) will later be compared to

similar data on available females.

Timing of female availability

When are females sexually available, i.e., outside of their burrows

and responsive to male signals? To answer this question, individual

Table 4. Sources of variation in <u>collustrans</u> male duration.

Variable	F value	Prob. >F	
number	47.18	.0001	Rsquare = 0.72

Crep did not meet 0.15 significance level for entry into the model.

Clouds did not meet 0.15 significance level for entry into the model.

Slope:
  number   0.01   (Duration increases ∿1 min per additional
                       100 males.)

Regression on dependent variable duration. Model: duration = number *
crep * clouds. significance level for entry into the model = 0.15, n =
20 nights. (Proc. Stepwise, SAS 1982.)

females were tracked throughout their adult lives. Figure 19 shows the distribution of available-female-minutes in 1983. Females were available from 12 to 33 MAS, with a peak in number available at 22 MAS. Figure 20 shows the distribution of available-female-minutes in 1982. Females were available from 6 to 52 MAS, and some of these females stayed out past 60 MAS (not shown). Peak numbers were available at 24 MAS. These same data were converted to crep units to produce Figs. 21 and 22.

There is an obvious difference between 1983 and 1982 frequency distributions. In 1983, females did not stay available as late in the evening as females in 1982. The reason for this difference will be explored below.

Keeping track of individual females night after night produced data on how, if unmated, females changed the timing of their availability on subsequent nights. (If mated, there were usually no subsequent appearances.) Females in 1982 went for as long as 10 nights without mating. Figure 23 shows that these females came out earlier on successive nights, a phenomenon predicted by Lloyd (1979b). Such behavior is likely to increase the duration of overlap with male activity. However, this strategy is not without accompanying risks (see chapter on risk of predation).

Comparison of male and female timing

In this section the timing of female availability is compared with that of male mate-locating activity. The female availability data are presented in both MAS and crep units for each year they were studied, 1982 and 1983 (presented above in Fig. 19 through 22). The male activity data taken in MAS during 1983 (Fig. 16) are compared with MAS

female data, and the combined male data in crep units (Fig. 18) are compared with the female crep data.

1983 females. The comparison of 1983 males with 1983 female data in MAS (Fig. 24) shows (1) male activity began slightly before the start of female availability, (2) the time of greatest male activity corresponded generally with the time of greatest female availability, and (3) the number of females available dropped to 0 slightly before the end of male activity. This is more-or-less the case predicted in Walker (1983a) for a situation where females eclose over a 24-hour period, but all become available to mate at a certain time of day. Such appears to be the case with collustrans females. This 1983 female curve shows what happens when males are abundant. Most females mated the first night out, within a few minutes of leaving their burrows (see Lloyd 1979b). The pattern is similar when the female data are converted to crep units and compared to male availability data in creps (Fig. 25).

1982 females. Quite a different picture emerges from the comparison of 1982 female availability with male activity. Figure 26 shows the MAS comparison with 1983 male data. Once again, the start of male activity preceded the occurrence of female availability. However, the number of males active declined rapidly at about the time female availability was at its peak. In other words, a large proportion of female availability occurred long after male activity ceased. The same basic pattern is seen in the crep comparison (Fig. 27)

On 87 occasions females stayed out after male activity ceased (1982), yet no mating was found to be initiated after males stopped for the night. This does not completely rule out the possibility that males do on rare occasions find females after male signaling flights end.

(For example, a male that perched for the night might walk to a female glowing nearby.) However, it does seem reasonable to pursue other explanations for why females were available when males were apparently not active.

Although not unique (see Roberts 1971, Rutowski and Alcock 1980), this situation seems to be a paradox from either the male or female point of view. One would generally not predict that males would cease their activity with so many potential mates available. Nor would one predict that females would stay out after male activity ceased, especially if it is dangerous to do so (chapter on risk of predation).

The timing of the end of male activity may be the easiest to understand. Regardless of the number of females available, males probably stop searching when the available light drops to a certain level (Lloyd 1966; Adams 1981, 1982). Finding that males stop earlier when it gets dark earlier (Table 3) supports this notion. The eyes of collustrans males are adapted to searching in the failing light after sunset (Lall et al. 1980). It may be that as the ambient light level drops, collustrans males become unable to see and avoid obstacles in the flight path (see Lloyd 1979b).[6] Male eyes may be specialized to maximize perception at the beginning of the activity period when the number of potential mates is highest (see Lall et al. 1980). As seen in Fig. 24 through 27, early evening males unable to search later have potential mates regardless of male density. However, a hypothetical male that searches later but is unable to search in the early evening

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[6]If collustrans males are unable to see obstacles or predators (Lloyd and Wing 1983) in darkness, this explains why they could not search for females after the signaling period as some crickets do (Walker 1983b).

would have mates only when early evening males are scarce (also see Dreisig 1971). If male eyes are adapted either to late or early evening, but not both, then it is not surprising that collustrans males would have evolved to search only in the early evening.[7,8]

Why did females in 1982 remain out after male activity had ceased?[9] Females became unreceptive and re-entered their burrows as soon as mated. But, when not mated, it seems that females "don't know when to quit." That is, females do not seem to recognize that it is no longer profitable to continue mating efforts due to a lack of active males.

If such fruitless extensions are maladaptive why don't females use the same cues as males to time their activity or merely stop when they no longer see males signaling? First, remember that females generally get into this situation (males have stopped, the unmated female is still out) only when males are scarce. So if a female does not see any males, it could be either because no males are in her vicinity (although males are still active), or because males have stopped for the night.

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[7]Photinus tanytoxus is a sibling species of collustans that becomes active as collustrans males stop for the evening. It would be interesting to know whether speciation in this case was connected to the visual specialization of tanytoxus for later and collustrans for earlier flights (Lloyd, pers. comm.).

[8]Lloyd (1979) suggests that males use the flashes of other males as an indicator of where to search, and a male that continues searching after the others stop may stray from the area. Because males only search for about 18 min per night, a lost male would have very little opportunity to locate a deme by seeking flashing males. If this is the case, gene flow between demes, which is already presumed to be limited because females are flightless, may occur only rarely. Because even seemingly trivial genetic differences can have major biological implications (see for example Wing et al. 1985), the differences between demes should be investigated (see Gross 1984).

[9]That these were indeed collustrans females seems clear because many mated with collustrans males on subsequent nights.

Therefore females would not be selected to retire in the absence of male signals. On the other hand, females might be lured into continuing to wait for a mate by the signals of a heterospecific male. Female collustrans apparently cannot discriminate signals of their own males from those of other species. Lloyd (1966) found that a collustrans female he moved to a P. umbratus site repeatedly answered umbratus males. I have observed collustrans females (n = 2) doing this at the study site, where umbratus also occur at the same time collustrans males are active. Lloyd also observed collustrans females answering P. tanytoxus males. I took 2 collustrans females that were out late to a nearby tanytoxus site, and they repeatedly answered males. Furthermore, 5 collustrans females at the study site would answer the first flash of almost any flash pattern made with a dim penlight, although they varied in how many signals they would respond to. One female even appeared to respond to the light of a passing motorcycle. Therefore, females seem unable to base a decision on retiring for the evening on either flashes they do see or flashes they do not see.

With respect to using ambient light cues to time retiring, females cannot rely on their micro-local light level to predict the levels their males experience. Males fly in a relatively open, homogenous habitat in terms of ambient light. Apparently, when it gets too dark to see obstacles, they quit. The flightless females, on the other hand, are perched on or near the soil surface. Some females are found on bare sand, others in grass of varying height and density, and some beneath the thick foliage of shrubs. The light level varies considerably from place to place in these microhabitats where females (presumably with the same ability to judge and react to light levels) are found. Therefore,

light level as a cue for when it is no longer advantageous to seek mates is not nearly so reliable for females as it is for males.[10]

The second factor in females staying out too late is that the loss of fecundity due to waiting another 24 hours to mate is a certainty (see chapter on energetic costs), whereas the risk in staying out too late (predation) is relatively low. Thus, if there is any doubt that males have stopped, a female might be better off to delay retiring.

To summarize, the degree of difficulty experienced in finding a mate varies considerably among collustrans females. Usually collustrans males greatly outnumber males of the few other species that are active at the same time of day. The collustrans female leaves her burrow in the midst of a dense cloud of searching males. She has but to flash a few times and she will be mated within seconds.

It is usually only during times when males are scarce that females are still seeking mates at the end of the male activity period. In this situation, females are caught between forces that dictate retiring and those that dictate staying out. At this time I am unable to suggest a better explanation than that females are without reliable information on which to base a decision. However, that a possible explanation has been offered should not close the issue. On the contrary, the question of why females are available when males are not active should be vigorously pursued. Anomalous phenomena, such as this, are of the greatest value in science, for they show where our models are inadequate.

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[10]Females may not use male flashes to cue when to leave their burrows either. On an unseasonably cold night in May males did not make signaling flights. I walked around with my penlight, and found 10 females. These were already perched outside of their burrows not coming out, when they answered. This is another example of females being available when no males were active (also see Dreisig 1971).
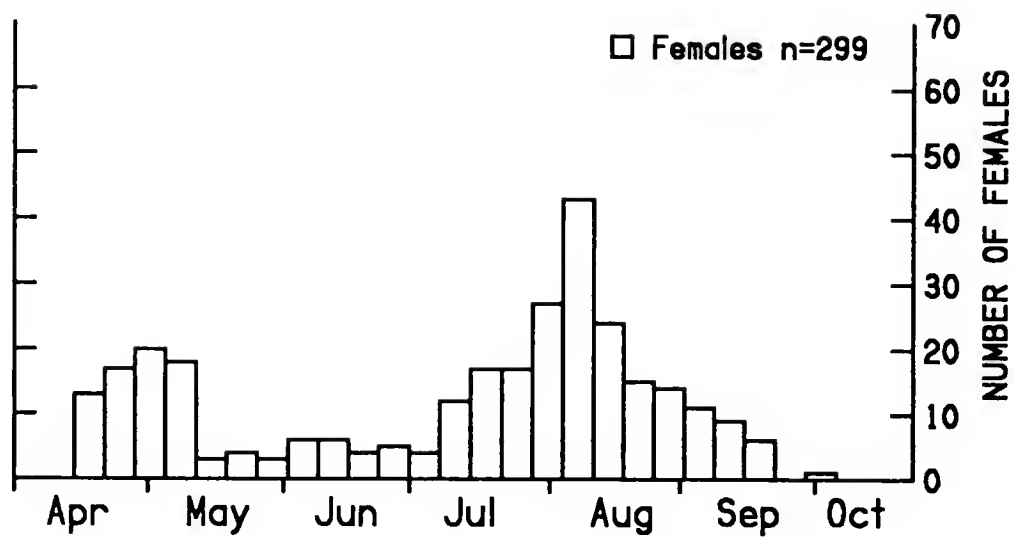
Fig. 14. Seasonal distribution of Photinus collustrans adults.
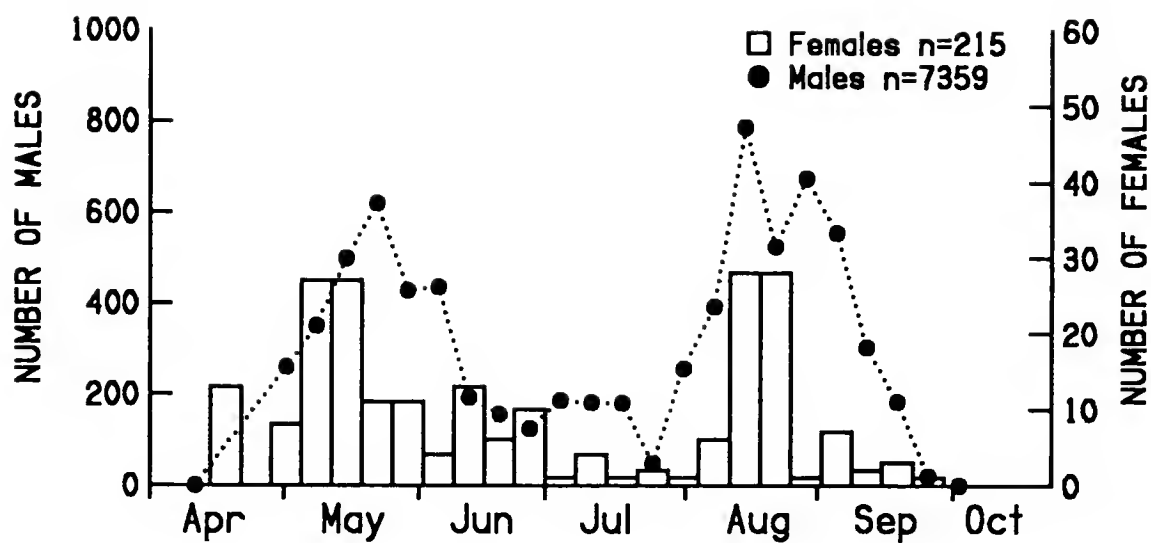a) 1982. Number of new females found per week (7 days per week search).

Fig. 14. Continued. b) 1983. Line: number of males crossing 50 ft transect per night. Bar: number of new females found per week (6 day per week search).
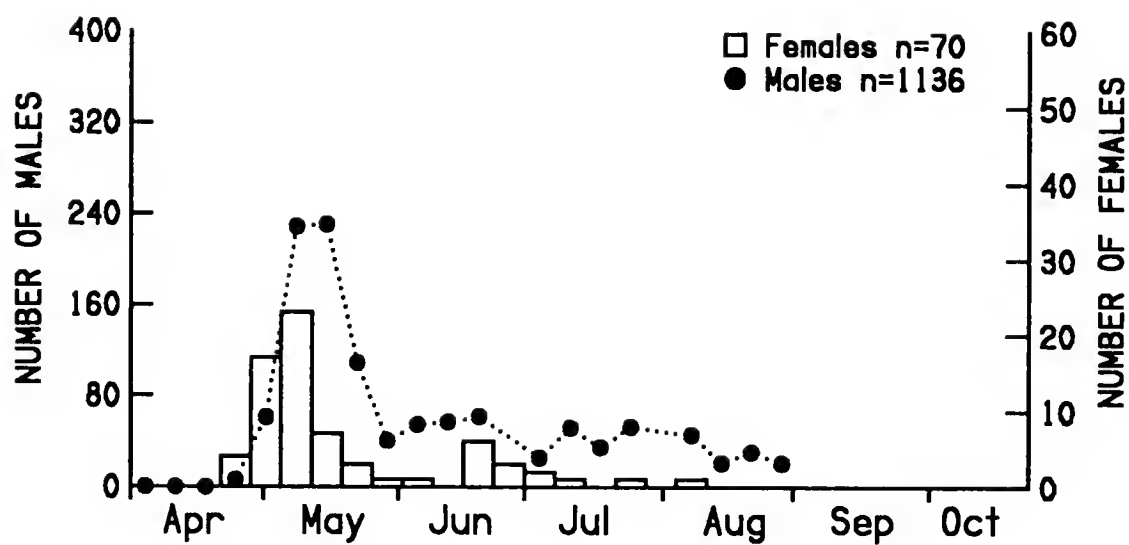
Fig. 14. Continued. c) 1984. Line: number of males crossing 20 ft transect per night. Bars: Number of new females found per week (6 days per week search).
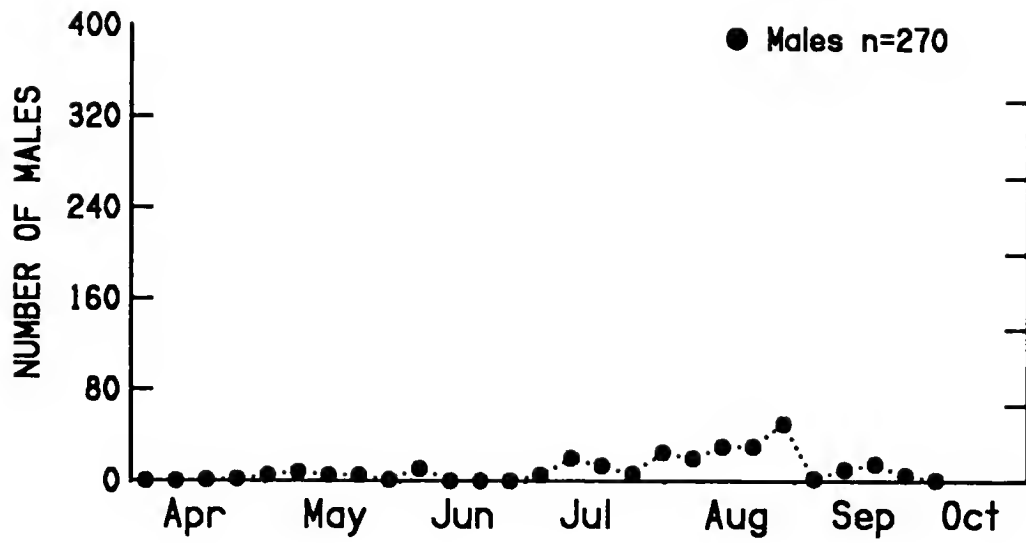
Fig. 14. Continued. d) 1985. Number of males counted or estimated at entire collustrans site.
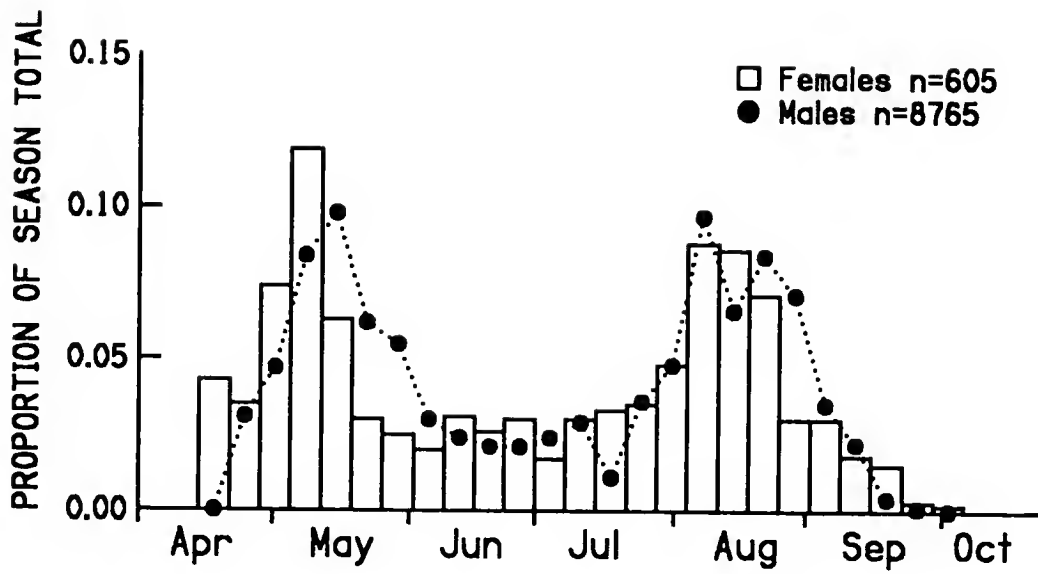
Fig. 14. Continued. e) Summation of data in Fig. 14a-d as proportion of seasonal total. Line: males Bar: females.
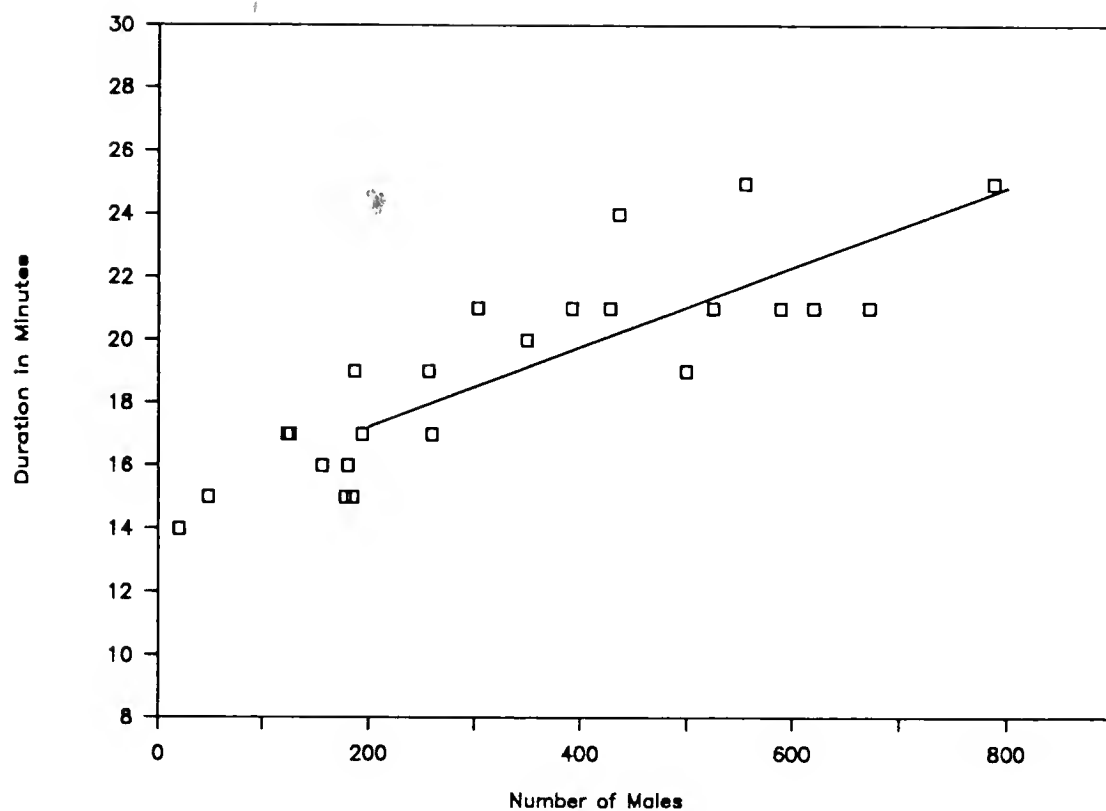
Fig. 15. The relationship between density of Photinus collustrans males and the duration of their activity period.
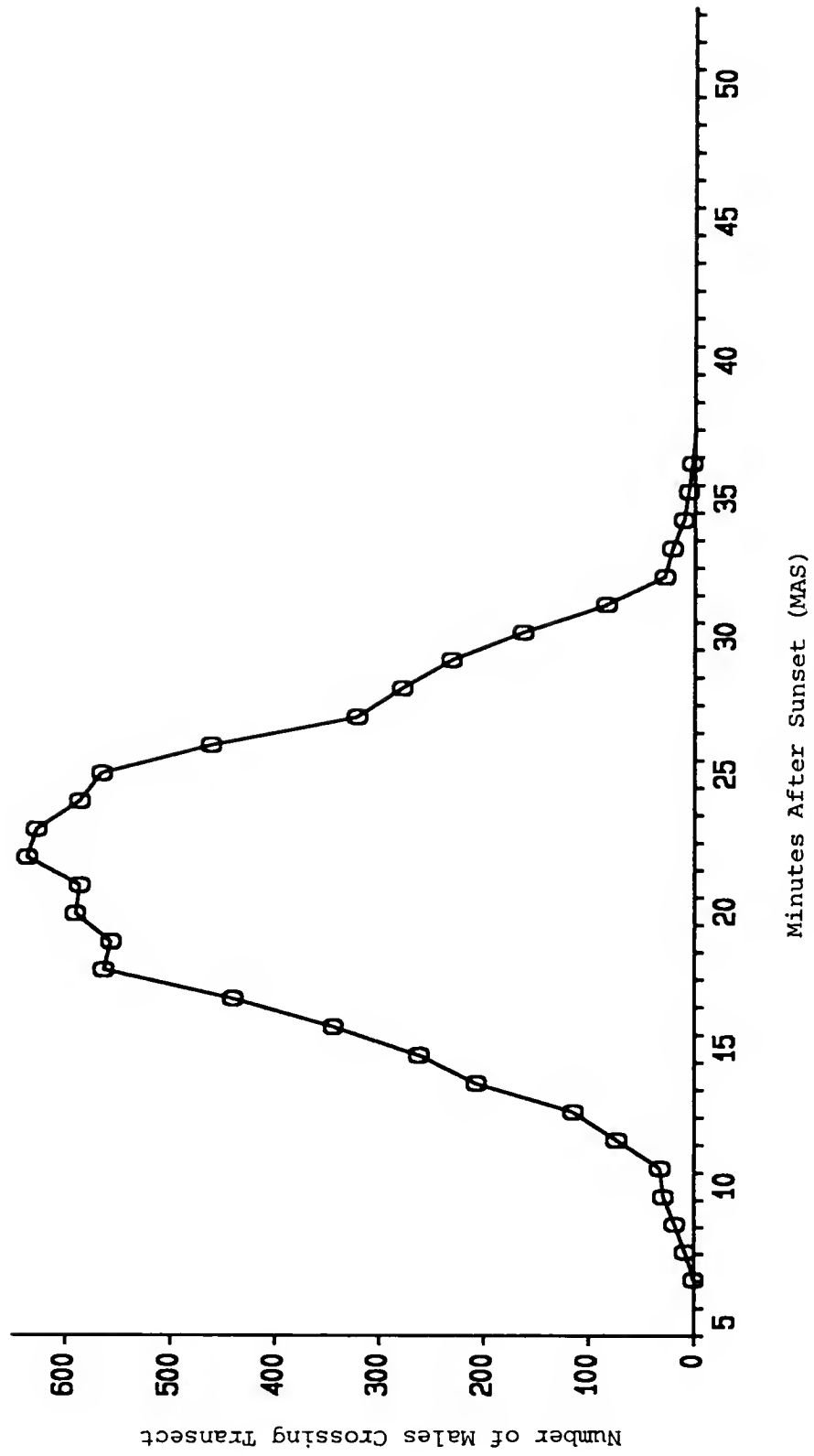
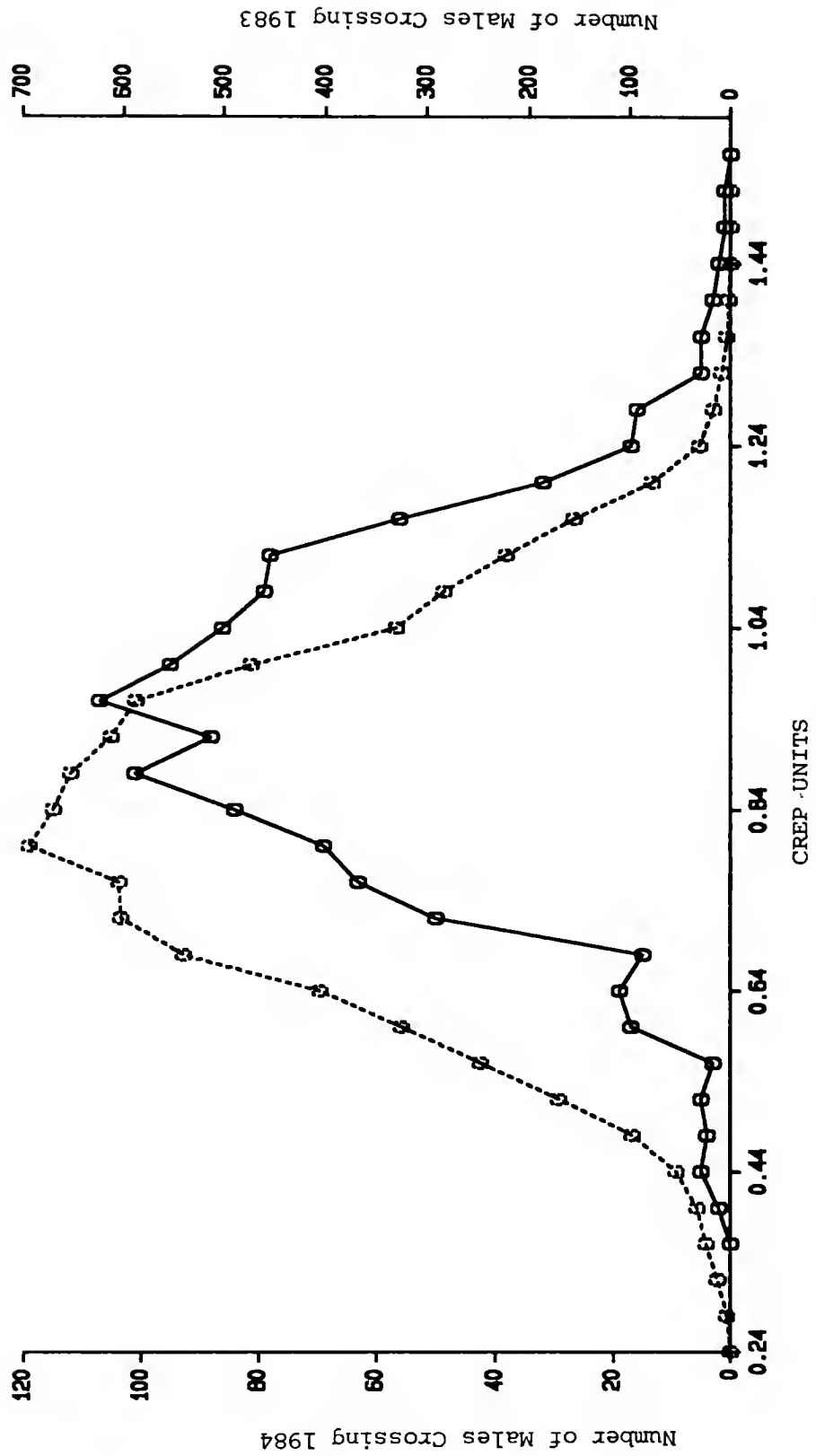Fig. 16. Temporal distribution of signaling males in Minutes After Sunset (1983).

Fig. 17. Temporal distribution of signaling males (1984) in crep units (solid line) and approximation of temporal distribution of signaling males (1983) in crep units (dashed line).
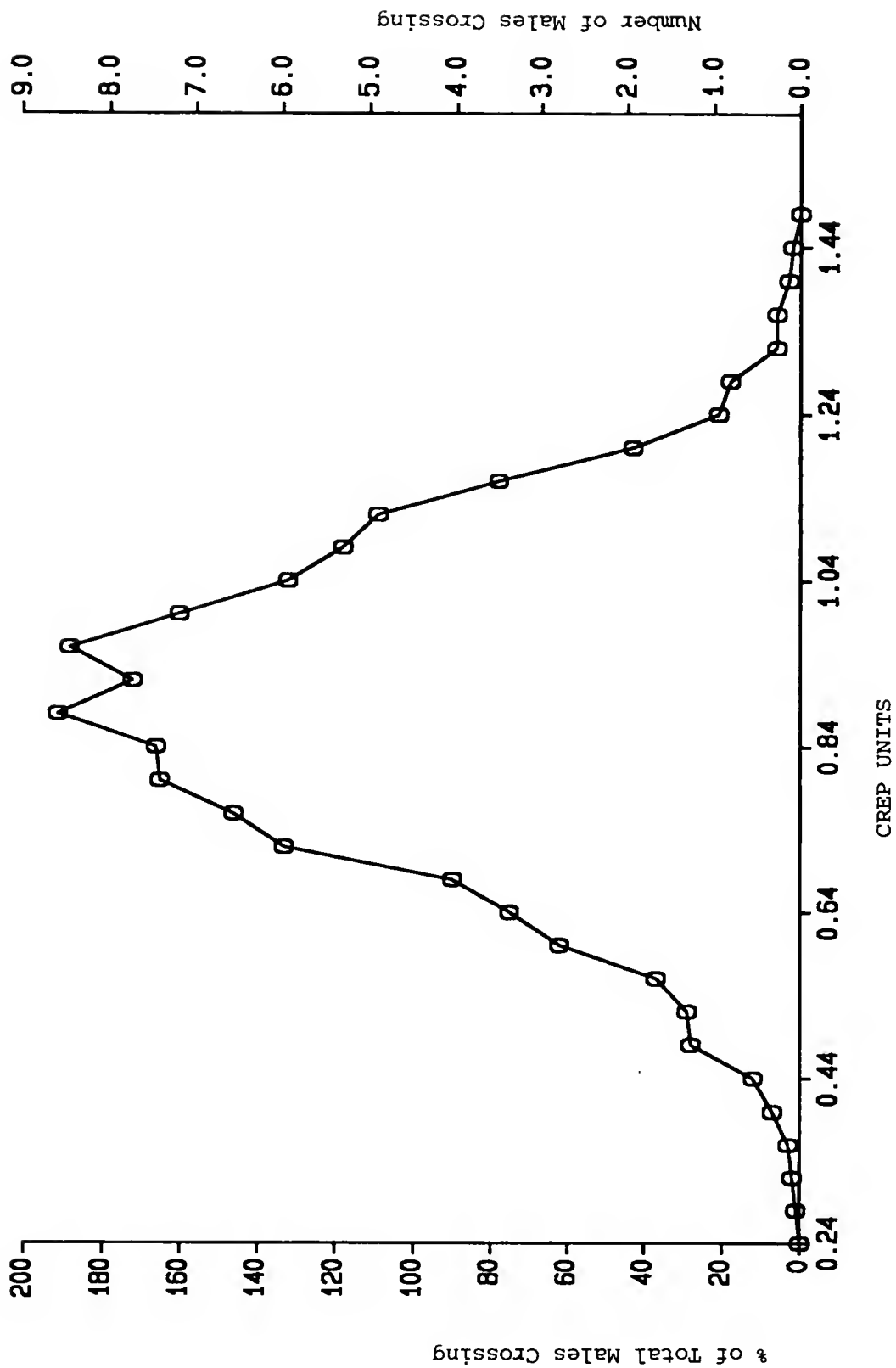
Fig. 18. Combined 1983 and 1984 data (equally weighted) on temporal distribution in crep units of signaling males in percent of total and number of males crossing.
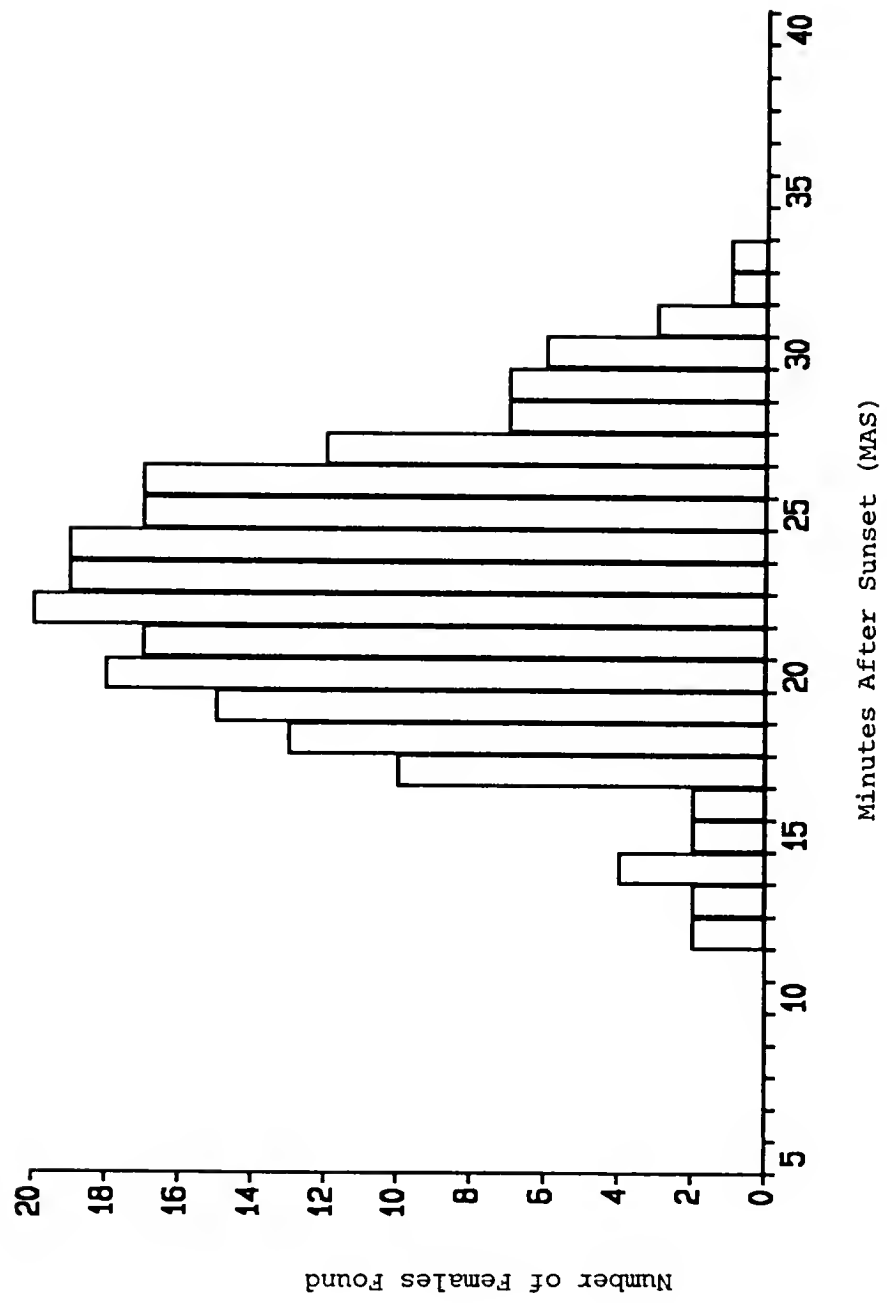
Fig. 19.   Temporal distribution of available females in Minutes After Sunset (1983).
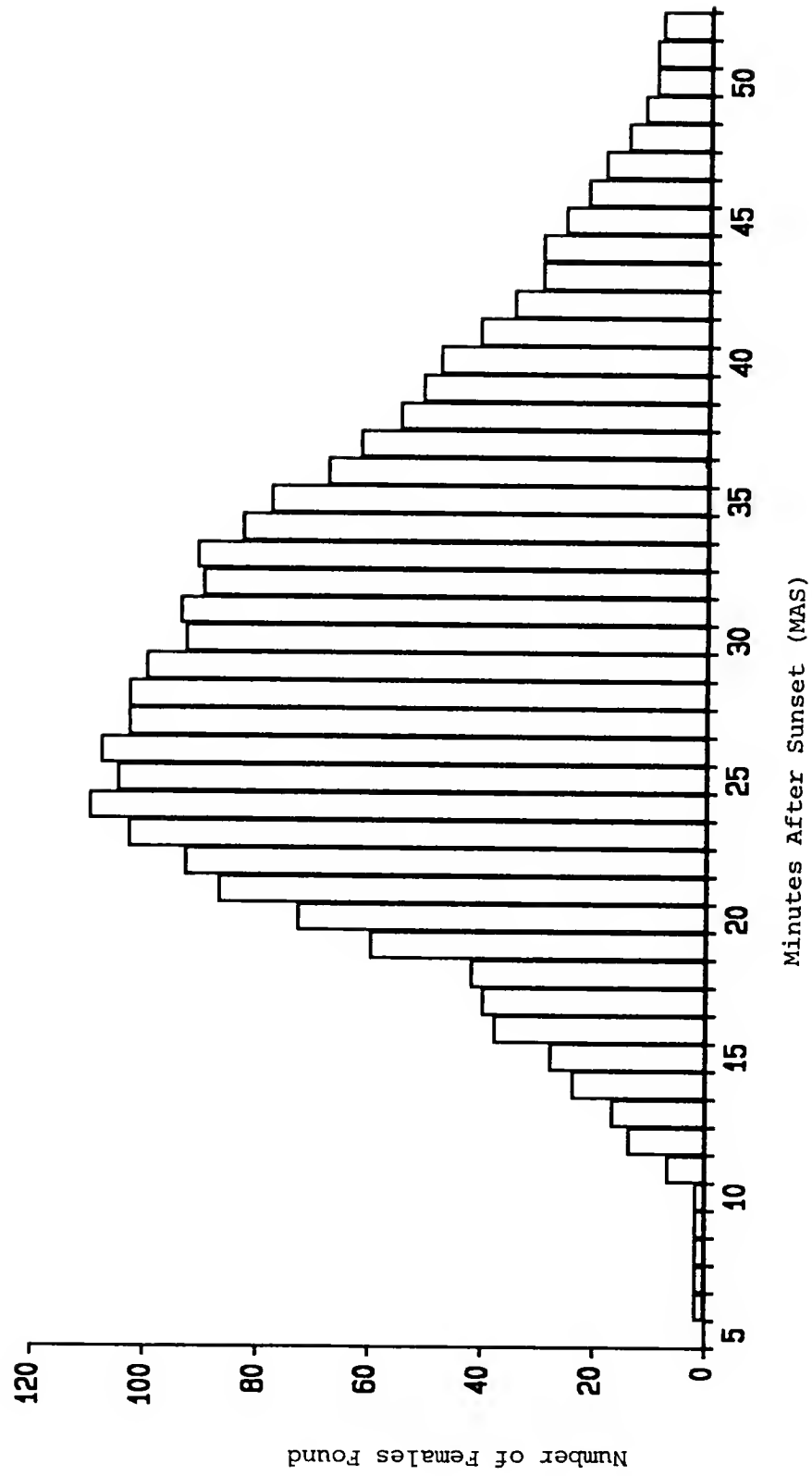
Fig. 20. Temporal distribution of available females in MAS (1982).
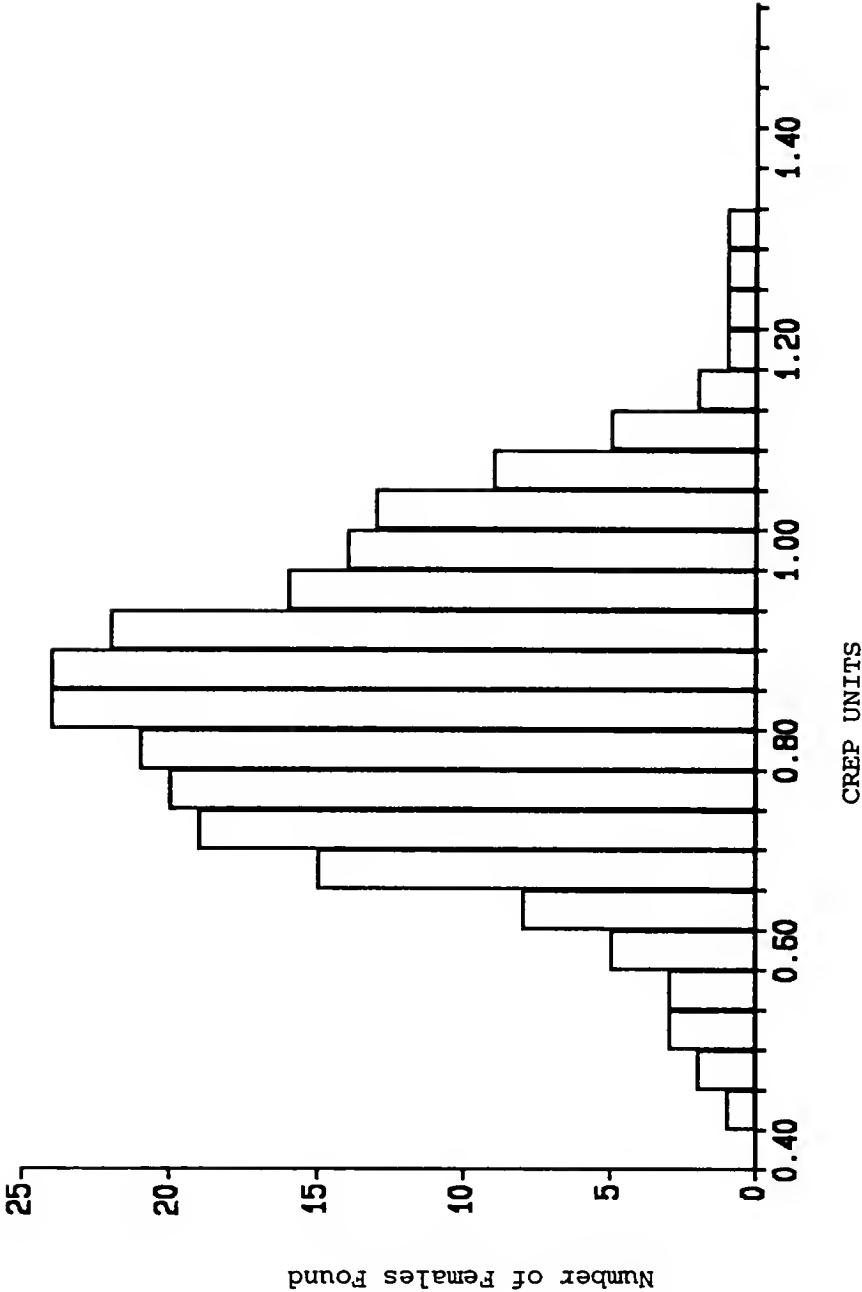
Fig. 21.   Temporal distribution of available females in crep units (1983).
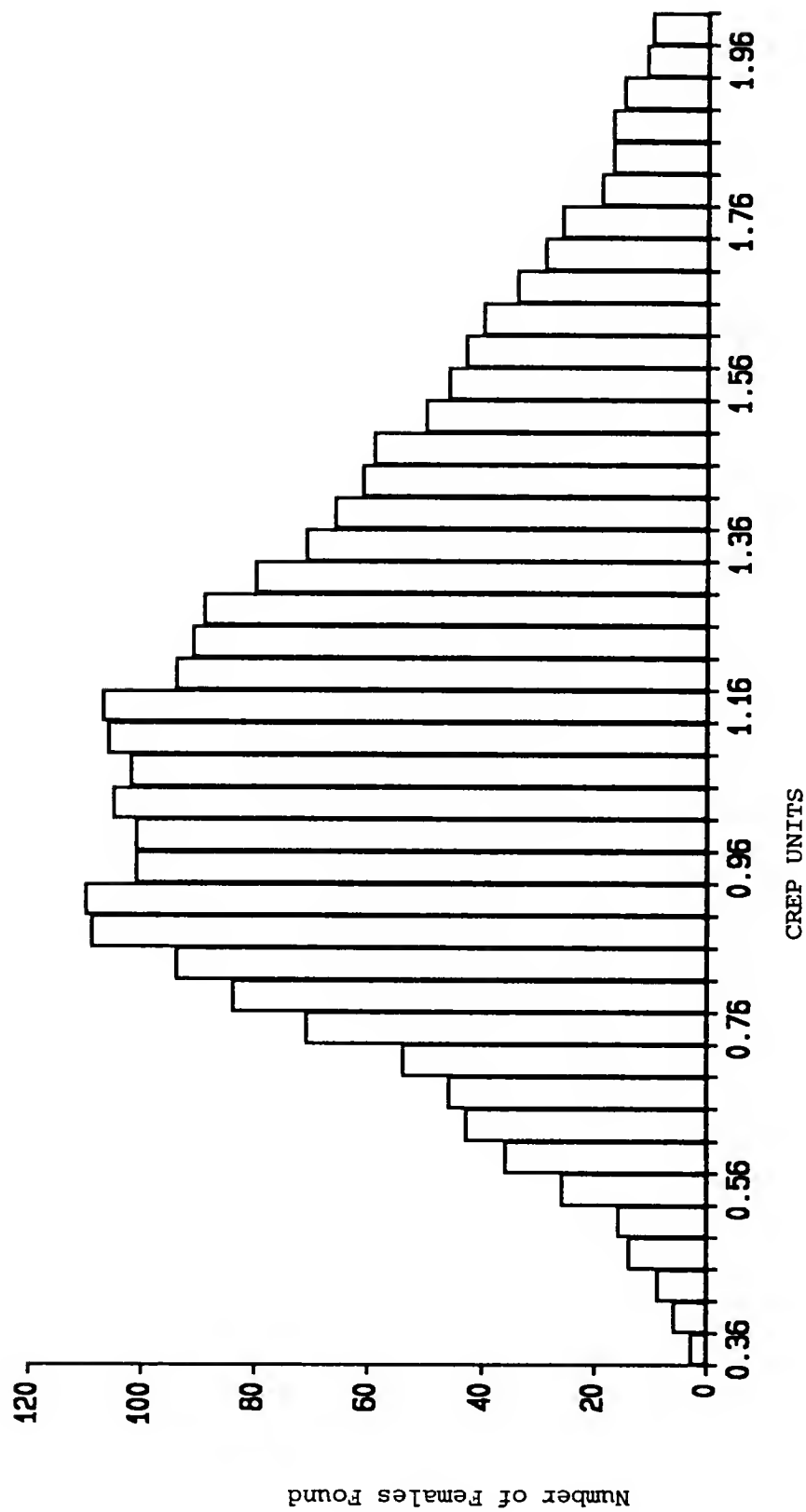
Fig. 22. Temporal distribution of available females in crep units (1982).
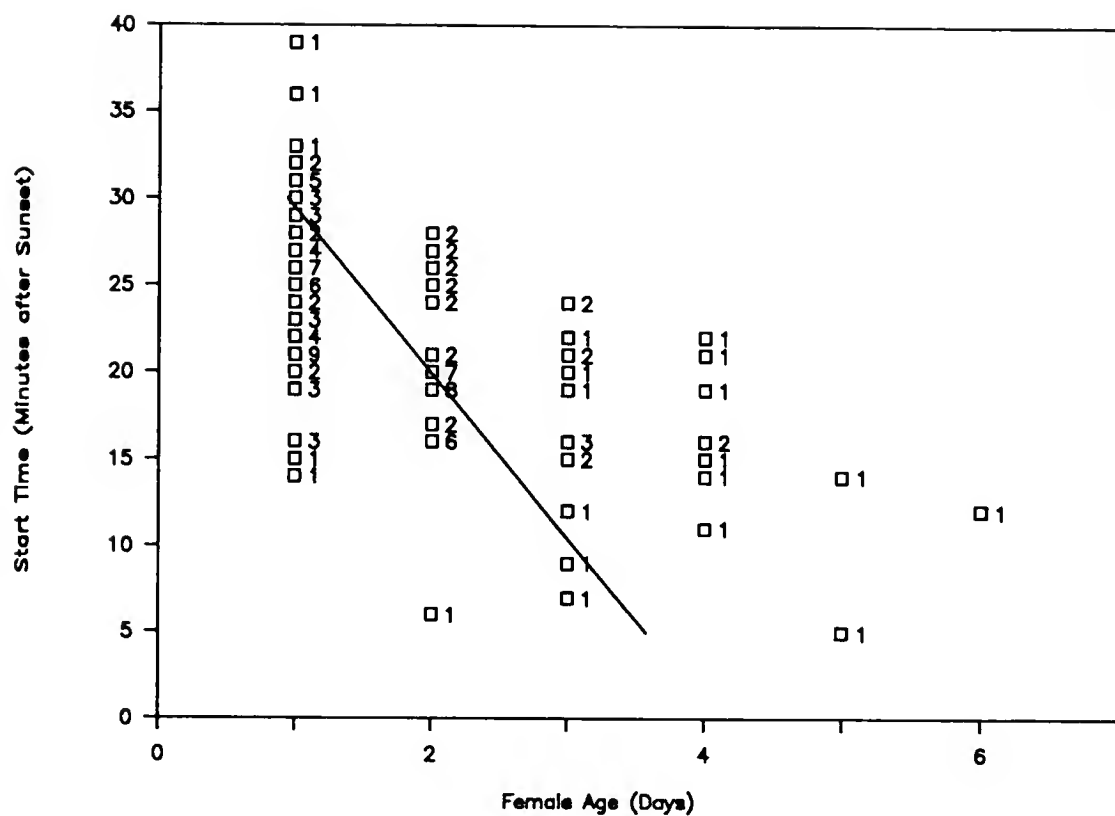
Fig. 23. Relationship of female start time to age. Numerals = number of observations at those coordinates.
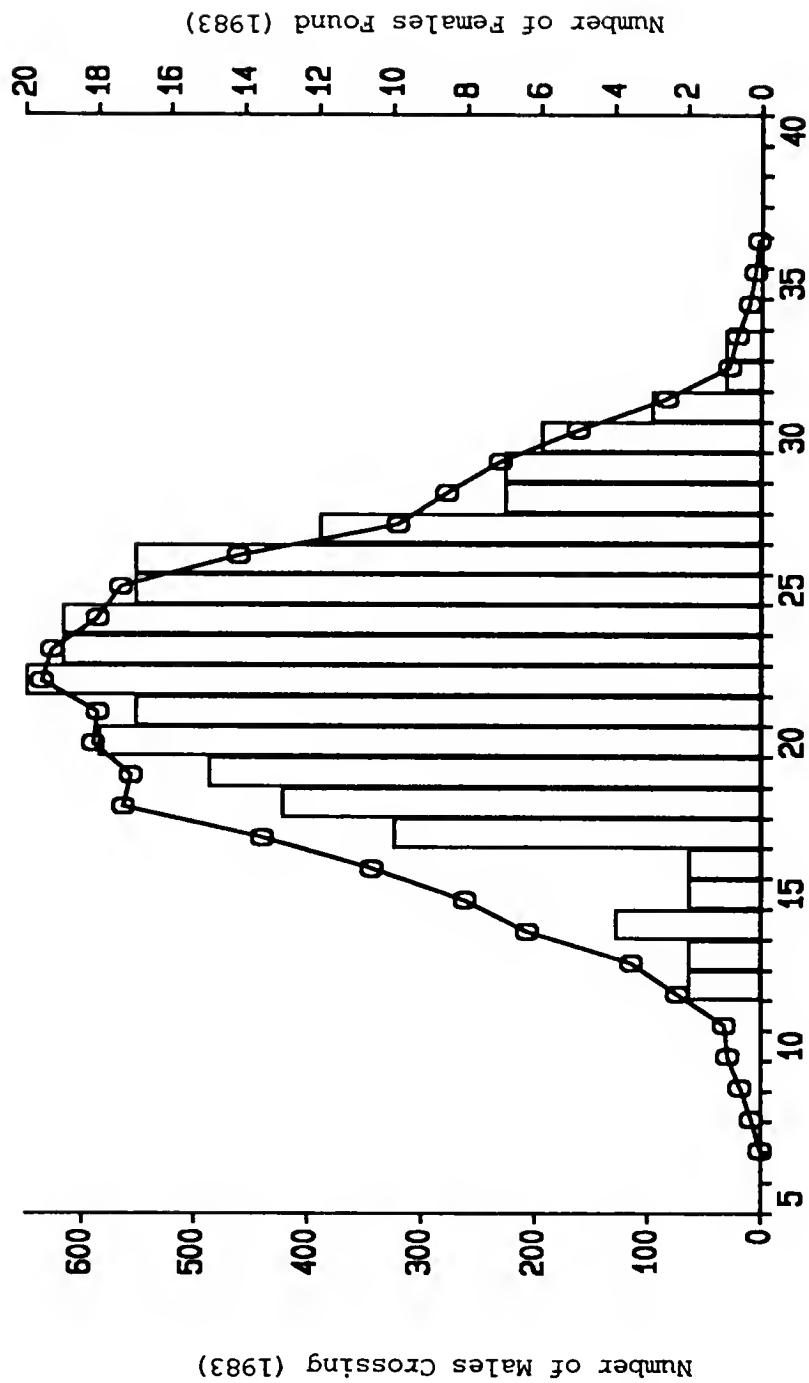
Fig. 24. Temporal comparison of female availability (recorded when males were abundant) and male searching activity, in MAS. Line: 1983 males. Bars: 1983 females.
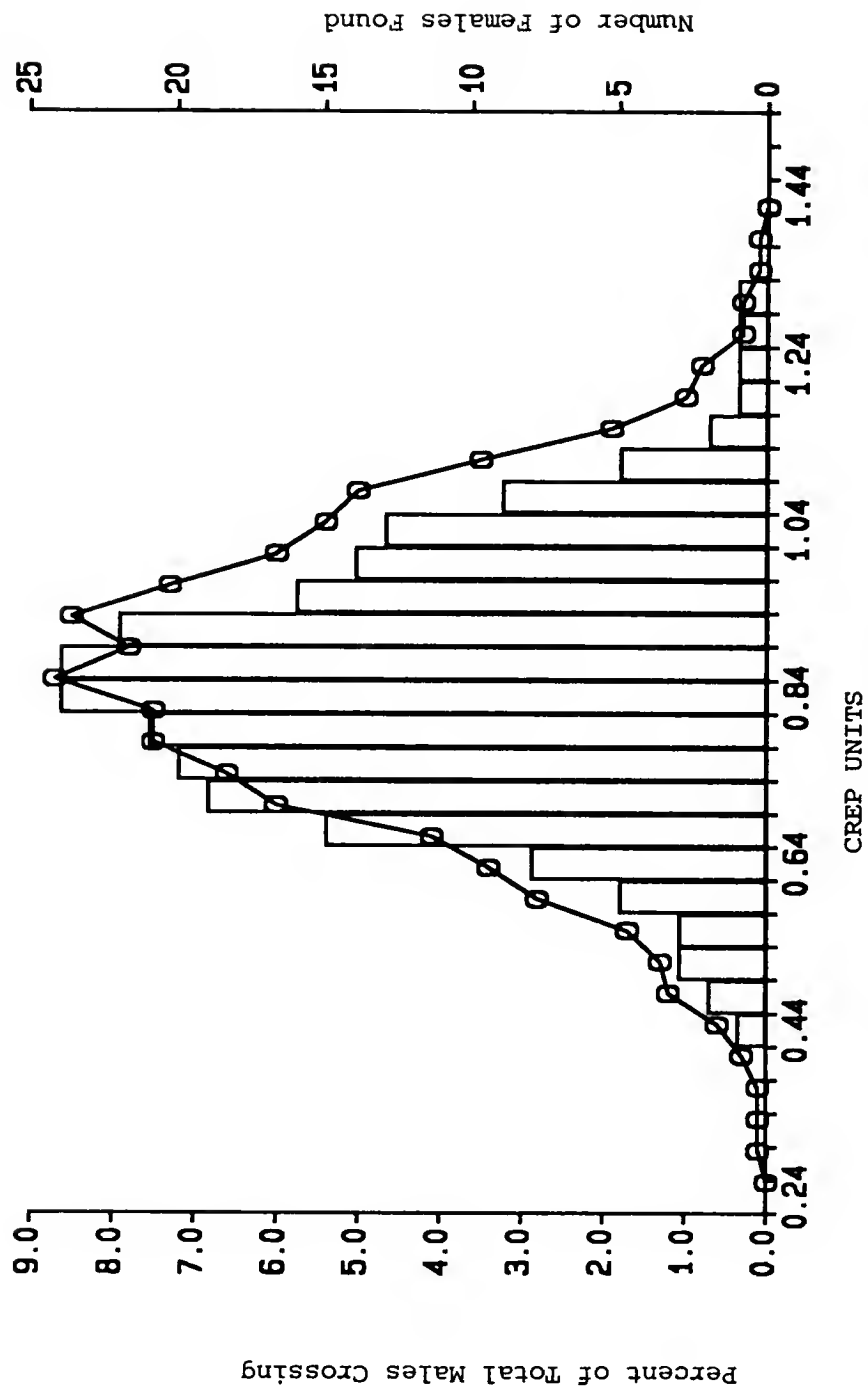
Fig. 25. Temporal comparison of female availability (1983) (recorded when males were abundant) and male searching activity (combined 1983 and 1984), in crep units. Line: males. Bars: females.
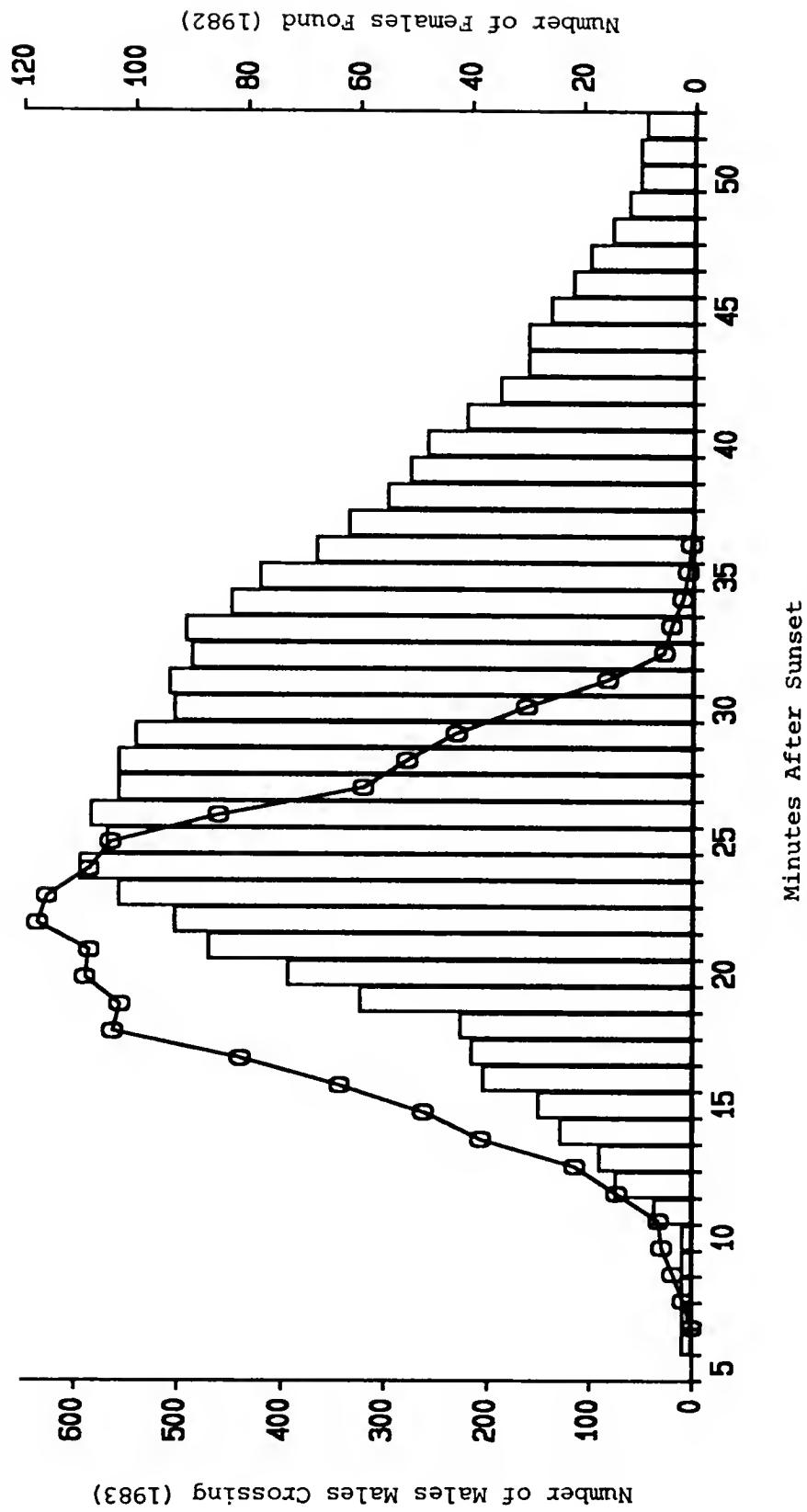
Fig. 26. Temporal comparison of female availability (1982) (recorded when males were scarce) and male searching activity (1983), in MAS. Line: males. Bars: females.
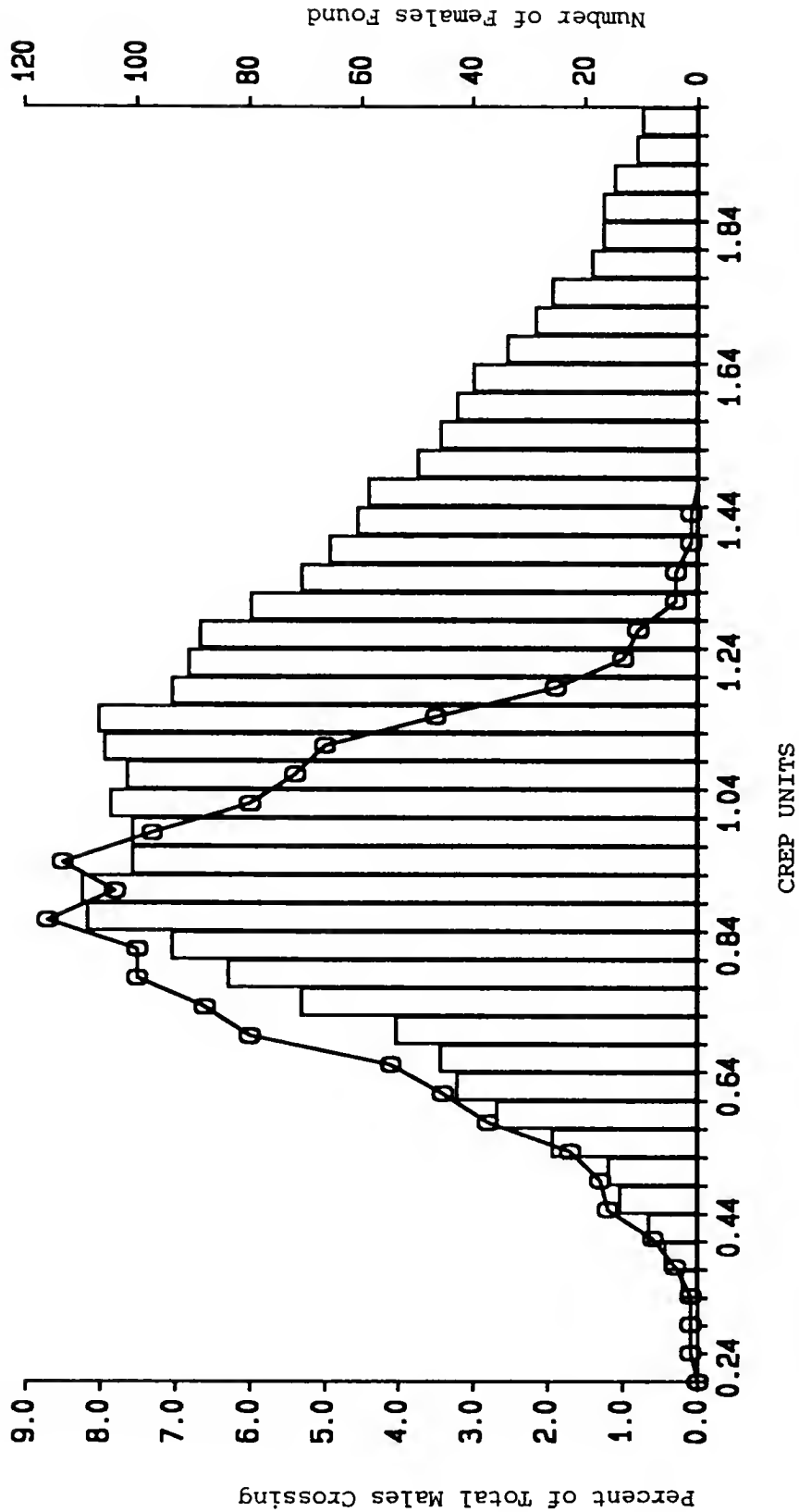
Fig. 27. Temporal comparison of female availability (1982) (recorded when males were scarce) and male searching activity (1983 and 1984 combined), in crep units. Line: males. Bars: females.

SUMMARY AND CONCLUSIONS

Aspects of the reproductive ecology of Photinus collustrans are
documented in these studies and the adaptive significance of these
characteristics is investigated. The soft bodied, flightless females of
this species spend most of their adult lives in their burrows in the
soil. Females experience an increased risk of predation when outside of
their burrows. For this reason, adaptations that allow females to
minimize the time spent outside of their burrows are not unexpected.
Females leave their burrows only for mating, and even then remain near
the burrow opening. The vast majority of females mate only once, and
copulation durations are brief by firefly standards. On their first
night out, female exits from their burrows correspond with the peak of
nightly male activity. Thus, a female may mate and return to the burrow
within moments of her first exit, never to leave the burrow again.

Risk of predation is not the only cost of mating for females. A
female that fails to mate must delay oviposition to accommodate mating
efforts on subsequent nights. The longer the delay, the fewer eggs will
remain to oviposit. Unmated females make subsequent exits from their
burrows earlier, overlapping their availability with more of the nightly
male activity period.

Females that are unmated at the end of the male activity period
often remain out long after male activity has ceased. In so doing

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females incur additional risk of predation while apparently having no chance of mating. This unexpected phenomenon has not been conclusively explained, and deserves further study.

Further study is also required to determine the cause of earlier male start times with increasing density. Observations of other males' signals could be a factor. Flashes of males flying on the previous evening and/or "warm up" flashes by perched males before the onset of the search period may be involved.

EPILOGUE: <u>COLLUSTRANS</u> IN PERSPECTIVE

Introduction

The purpose of this section is to summarize characteristics of <u>collustrans</u>' life history strategy and to make comparisons with other species. Among Lampyridae females of some species, including <u>collustrans</u>, are brachypterous, but other life history strategies of adult females occur as well (Lloyd 1966). These include winged flight-capable females, and apterous larviform females. This variety of life history strategies within the family poses questions for taxonomists (Cicero 1984) and behavioral ecologists (Fritz et al. 1982, Gross 1984) alike. In order to address questions regarding how and why the variety of female forms evolved, a data base concerning the behavioral ecologies of the different forms is required (Cicero 1984). Although beyond the scope of this project, an extensive survey of species representing each of the three types of adult female body plan (alate, brachypterous, larviform) would be valuable. Six characteristics that should be considered are:

1. Position on semelparity-iteroparity scale.

2. Adult mobility and related behaviors--dispersal, search for resources, and escape from predators.

3. Feeding or other nutrient acquisition as adult.

4. Adult lifespan.

5. Internal male reproductive structures.

6. Mating behavior.

There is a web of interrelationships among these characteristics, of which the egg laying pattern (semelparity vs. iteroparity) may be the key (see Fritz et al. 1982, and refs.). The criterion used by Fritz et al. (1982) "in defining semelparity and iteroparity in insects is the temporal pattern of egg maturation and deposition."

Almost by definition, iteroparity, which involves distributing egg maturation and deposition over time and space, requires mobility. To distribute eggs in space and/or to acquire nutritional supplies needed to extend the lifespan for distributing them over time would almost always require female mobility, although there are exceptions.

Females could acquire nutritional supplies by locating food and feeding, but nutrients might also be delivered to them by courting males. Such deliveries might take the form of nuptial feeding (Thornhill 1980) or nutritious ejaculates (Bowen et al. 1984). Among the fireflies nuptial feeding is unknown. As an indicator of the possibility of nutrients being delivered in ejaculates, the complexity of the male accessory glands is considered here. Little is known about the function of firefly accessory gland products, but such products in other insects are known to serve as nutrition (Boggs and Gilbert 1979). Other functions are also known in other insects (Parker 1970). Related to transfer of nutritious ejaculates is mating behavior, particularly copulation duration and female mating frequency. In fireflies the briefest known copulations apparently involve only semen transfer, whereas longer copulations involve transfer of complex ejaculates (Wing 1985). Female multiple mating would be expected when females acquire needed materials in the ejaculate, although it may also occur for other reasons (W.F. Walker 1980, also see Watanabe 1988).

Using these six characteristics here to compare species representative of each female body type will more clearly define the collustrans strategy.

Materials and Methods

Photinus umbratus, Pyropyga minuta, and Photuris spp. were studied at the collustrans site.[1] Photinus marginellus and Phausis reticulata were studied at Highlands Biological Station in Highlands, N.C. P. marginellus was found in the yard at Illges Cottage and nearby, and Phausis reticulata was found on the Rhododendron Trail.

Photinus marginellus and umbratus females are alate, and the same methods of study were used for both species. Perched females were located by their flashes in response to signals of flying males or to penlight flashes. The locations of females were marked with numbered stakes, and pair formations were observed. Copulation durations were determined by intermittent observations in the field. Males and females were dissected using standard techniques. Larvae were housed and fed in the same manner previously described for collustrans.

Data on longevity of alate females are drawn from records of the interval between capture and death or dissection of field-collected specimens of unknown age. These females were kept in vials with a cube of apple in the laboratory.

The larviform females of Phausis reticulata were located by their glows. Female locations were marked with numbered stakes. Some females were collected and kept in vials with soil and leaf litter from the

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[1]Also at this site numerous phengodids are found when the area is flooded (Wing 1984). Additional studies of Photuris spp. were made at the nearby macdermotti site (Wing 1982).

site. Males were netted as they flew glowing through the forest, and were housed in vials with damp leaves. Matings were arranged by placing a male in the vial with a glowing female. Some males were dissected.

Results and Discussion

Species with Brachypterous Females: Photinus collustrans

In considering the subject of iteroparity vs. semelparity, three questions should be addressed (Fritz et al. 1982). First, are eggs deposited in different places? Second, are the eggs deposited at different times? Third, are eggs matured at different times?

As has previously been discussed for collustrans, the eggs are all deposited in one place (the burrow) and at one time, a single oviposition bout lasting a few days.[2] Evidence from 15 dissections indicates that all eggs are matured at once. In five of the females a few of the eggs were not yet quite full sized, but in no case were eggs found in early stages of development. (As noted in chapter on energetic costs, mature egg count was $\bar{x}$ = 71, range = 30 to 112, SD = 23.)

Other characteristics also suggest semelparity. While collustrans females are capable of some movement, they use this ability only in brief exits barely outside of the burrow for mating. No evidence of feeding by collustrans females has been found. They are not equipped to hunt underground as their larvae do, or to search for food outside the burrow. Male collustrans deliver only semen to females in their very brief matings and male reproductive systems are correspondingly simple

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[2]The small percentage of females that do return for a second mating a few days after the first probably deposit part of the complement of eggs after the first mating, and the rest after the second. One female that was dissected after returning for a second mating contained only 18 eggs.

in structure (Wing 1985). Furthermore, the vast majority of females mate only once. Thus, it seems unlikely that the ejaculate is a significant source of nutrition for collustrans females.

All of these characteristics support the classification of collustrans as semelparous.

Species with Winged Females

The representatives of species with winged females for this comparison are a congener of collustrans, Photinus macdermotti, and 2 Photuris species. Photinus macdermotti will be considered first.

Other alate firefly females have not been monitored 24 hours a day for life in the field to determine oviposition patterns (reviewed in Buschman 1977),[3] and the same is true of Photinus macdermotti females. However, on the question of egg maturation there are some data. Some females, presumably recently eclosed, contained no mature eggs or oocytes in intermediate stages of development. Other, presumably older females, contained all stages. In each of 8 females, eggs in all stages of development were found, and there was a wide range in number of mature eggs (range = 10 to 93, $\bar{x}$ = 34, SD = 28). This may reflect different ages or other circumstances among these field-collected females.[4] These data indicate that macdermotti females are capable of maturing eggs over time, and so iteroparity relative to collustrans is suggested. This is further supported by data on mobility.

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[3] I have not surveyed and analyzed published laboratory data, but some are indicative of alate female iteroparity. For example, Buschman's (1977) laboratory data indicate that some Pyractomena lucifera females oviposit several clutches of eggs over a period of several weeks.

[4] Photinus marginellus (n = 3) also had eggs in developing stages, which may be characteristic of winged Photinus females in general.

Female macdermotti are known to move about in the field. Marked females were found in different locations from night to night, and on two occasions females apparently moved to where males were (Wing 1982). By contrast collustrans females remained at their burrow night after night, even when it was located under dense shrubbery where there was almost no chance of being found by males. The mobility of macdermotti females suggests that they are able to distribute eggs in space.

Female macdermotti probably acquire very little nutrition by feeding. They apparently use their mobility to acquire water from the underside of leaves (Wing 1982), and they could travel to other food sources as well. However, no food was noted in the guts of dissected females. (Food is obvious in the guts of predaceous fireflies, below.)

A more likely source of nutrients is the ejaculate of males. Male macdermotti are characterized by complex male accessory glands (Wing 1985).[5] As would be expected, these glands produce ejaculates that are more complex than those of collustrans (Wing 1985). P. macdermotti copulations are prolonged, at least in part, to accommodate the transfer of the complex ejaculates (Wing 1985).[6] These macdermotti couplings last for hours, compared to about a minute for collustrans. Although the functions of the macdermotti male products are unknown, and there

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[5]Other species with alate females that share this trait include the Photinus species marginellus and umbratus; Pteroptyx valida (Wing 1982, Wing et al. 1983); and Pyropyga minuta. A previous pilot study of species from several genera (Lloyd and Dong Ngo unpublished) indicates that as a general rule species with alate females have complex male accessory glands.

[6]Prolonged couplings also characterize other species with winged females, including Pteroptyx valida (Wing et al. 1983), Photinus marginellus (n = 2, ∿1.5 h and ∿1.75 h), and Photinus umbratus (n = 1, >12 h but < 15 hr). Also see Dewsbury (1985) for a contrasting comparison of rodent male products and copulation durations.

are certainly a variety of possible functions, one possibility is that they are a source of nutrition to females. Consistent with this notion is the fact that macdermotti and other alate Photinus females are much more likely to mate repeatedly than are collustrans females (Wing 1985, Sara Lawrence unpublished).[7]

Photinus macdermotti females also seem to live longer than female collustrans. Seven macdermotti females survived 2 to 4 weeks in the laboratory after being collected at unknown ages. By contrast, collustrans females survive only about 10 days (Wing 1982).

The characteristics of macdermotti females suggest that they have a greater opportunity to mature eggs over time and to distribute them at different times and places than do collustrans females. An even more iteroparous example may be provided by the genus Photuris.

Photuris species of the versicolor-pennsylvanica group represent extremely mobile forms of firefly females. This mobility is utilized for hunting, which includes aerial predation of other fireflies (Lloyd 1984 and refs., Lloyd and Wing 1983). Thus, they acquire substantial nutritional resources that could be used for egg production, and they are capable of moving from place to place where they could oviposit.

Photuris are also extremely long lived by firefly standards. Four Photuris "D" females survived 4 to 8 weeks after capture with no prey to feed on. They are also apparently capable of maturing eggs over time. Six Photuris versicolor females were dissected, and all were found to

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[7] Photinus umbratus females may represent an extreme in Photinus female multiple mating. Females are usually found perched on the tips of grass blades, facing upward. When investigating responses to penlight signals, in 8 cases I found a female already in copula. In 4 other cases the female was copulating and a second male was standing by. In only 5 of the 17 cases did I find a solitary female.

have eggs in developing stages. (Number of mature eggs range = 10 to 45, $\bar{x}$ = 24, SD = 13.)

The extreme mobility, long lives, and rich diet of <u>Photuris</u> strongly suggest that they are among the most iteroparous fireflies.

Species with Larviform Females

A pilot study of <u>Phausis reticulata</u> provided some data on a species with larviform females. Nothing is known of egg maturation patterns in <u>Phausis reticulata</u>, and the only data on the egg deposition pattern comes from one captive female. She was housed in a zipper vial with soil and moist leaf litter. During one 24-hr period she deposited a clutch of eggs on the ventral side of her own abdomen (Fig. 28). She was able to carry the eggs in this location using her legs anteriorly and the tip of her abdomen posteriorly to move along with the abdomen arched, preventing contact between the substrate and the eggs. By the next day, only one egg remained attached to her. It is possible that individual eggs from a clutch end up scattered in different locations, one of the criteria for iteroparity. However, that eggs are produced in a group rather than singly suggests semelparity. Whether more than one clutch is produced is unknown.

Some observations were made to discern the extent of <u>Phausis</u> female mobility. In an area that was searched nightly, the positions of two <u>Phausis</u> females were marked the first night they appeared there.[8] The females remained stationary and glowing. Both were monitored until a

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[8]The asymetrical arrangement of light organs or "portholes" on <u>Phausis</u> females may appear to be sufficient to identify individuals, so that marking is unnecessary. However, observations of one female in captivity indicate that glowing females do not always use all of the same lights. Thus, the same female may show different patterns at different times (see Lloyd 1965).

half hour after the last male was seen. Neither female appeared at these marked positions on subsequent nights, nor were they found elsewhere. No evidence of a burrow was discovered at the sites of any of four females that were observed in the field. One of the four was found on a tree trunk about 1/2 meter above the ground. Sivinski (unpublished) watched a female move to the top of a log for mate attraction. These observations indicate that Phausis females may be somewhat more mobile than are female collustrans.

Although it is not known whether Phausis reticulata females feed as adults, the larviform condition suggests that they may continue to use larval food sources (see Schwalb 1961). Data from one Phausis female indicate an adult lifespan at least as long as that of collustrans females.

Phausis reticulata males have accessory glands that appear more complex in structure than those of collustrans, though not as complex as the macdermotti-like Photinus species (Fig. 29). What little is known about mating behavior indicates that Phausis reticulata copulations are of intermediate duration. A Phausis reticulata female in captivity mated with a captive male for 5 min, 5 sec. A few days later, after depositing eggs, the same female glowed and a different male was introduced into her vial. Copulation lasted 3 min, 32 sec. At the same location, Sivinski (unpublished) observed a copulation in the field that lasted about 20 min.[9]

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[9] Phausis reticulata couplings occurred with the male mounted on the female's dorsum, as collustrans do. This may be the norm for flightless female fireflies (see Wing 1985, Schwalb 1961).

Although these few data are not conclusive, they suggest that
Phausis reticulata females are equipped to scatter their eggs in space
and time to a somewhat greater extent than _collustrans_.

Conclusions

These comparisons clarify how extreme the modifications are that
minimize the adult role of female _collustrans_. They are mobile enough
to move a few millimeters to obtain sperm, but are not equipped to
disperse, or to search for resources such as food, oviposition sites, or
better places to locate mates.[10] Their ability to flee from predators
is very limited. As adults, females are short lived and exhibit a
limited behavioral repertoire, including minimal courtship and mating
behavior.[11] (Almost all females appear to accept any male that mounts
(Wing 1982), and females generally mate only once.) Female
collustrans stay in the burrow except for nightly mating attempts and,
once mated, they oviposit and die in the burrow. A reduced adult role
is not unexpected in a semelparous insect. In fact, one explanation for
the evolution of semelparity is that it occurs when the probability of
larvae surviving to adulthood is greater than the probability of adults
surviving to reproduce again (Fritz et al. 1982 and refs.). In
collustrans, larvae that become females seem to have responsibility for
all feeding, any dispersal that is done, and probably the selection of

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[10]Lloyd (pers. comm.) has long suspected the existence of occasional
winged females. Though not able to fly, Fig. 30 shows a female with
some of the traits of alate forms including one wing and darkened
patches of cuticle. She mated and deposited viable eggs.

[11]One way to further reduce the female role would be to eliminate
mating. If such asexual forms existed, would they be detected?

the burrow (pupation) site (which is the location for mate attraction and oviposition). One way to equip an adult female for these activities would be with a larva-like body, such as Phausis females have.

That Phausis reticulata have intermediate male accessory glands and copulation durations seems clear.[12] In the other traits compared here, data are not conclusive, but Phausis females may combine the reproductive function with the larval lifestyle. They may be able to feed and probably do seek out sites for mate-locating and oviposition to some extent. No evidence presented here contradicts the prediction that flightless female insects such as Phausis will be semelparous (Fritz et al. 1982), but a more iteroparous strategy than collustrans' has not been ruled out. It does appear likely that the adult role of females is more complex in Phausis than in collustrans.

Another way to develop the adult role is to invest in a radically modified, alate body. The flight-capable females considered here utilize their vagility in many aspects of their complex roles as adults. It may be instructive to consider how diverse the strategies are among different species with winged females. At one extreme are Photuris species, females of which utilize complex behavioral tactics in hunting. They are strong fliers, voracious predators, long lived, and are probably among the most iteroparous fireflies, scattering eggs over time and space. Photinus macdermotti females are probably moderately iteroparous, and their role as adults is probably of intermediate complexity. At the other extreme are species with fully alate females

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[12]Phausis therefore presents an interesting subject for further comparisons designed to elucidate the functions of these glands in fireflies.

that are far more semelparous. For example, some _Photinus_ females develop such a large clutch of eggs that they are unable to fly (Cicero 1983), and these may be as semelparous as _collustrans_.[13] A lesser diversity of strategies may occur among species with brachypterous females and among those with larviform females.

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[13]Such females could represent a stage in the evolution of brachyptery (see Liebherr 1988 and refs.).

Fig. 28. Phasuius reticulata female carrying eggs that she deposited on the ventral side of her abdomen.

Fig. 29. Internal male reproductive structures of (a) *Photinus macdermotti*, (b) *Phausis reticulata*, and (c) *Photinus collustrans*.

A.

← extends approximately 7.4mm

spiral gland

accessory glands

seminal vesicle

vas deferens

accessory gland

ejaculatory duct

0.5mm

B.

vas deferens

ejaculatory duct

0.3mm

C.

vas deferens

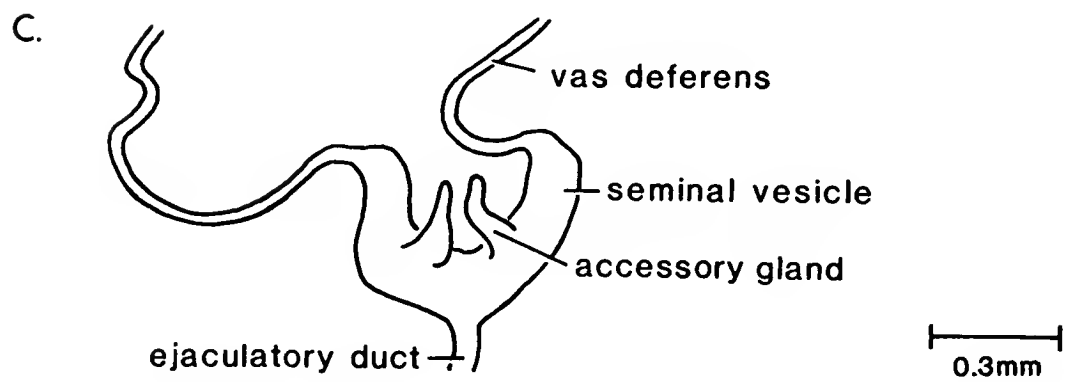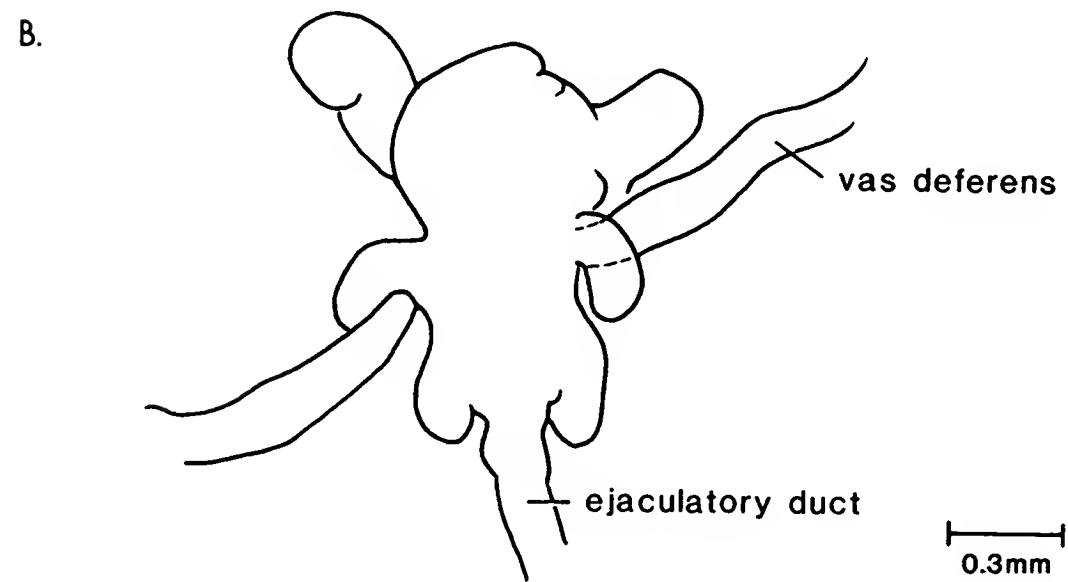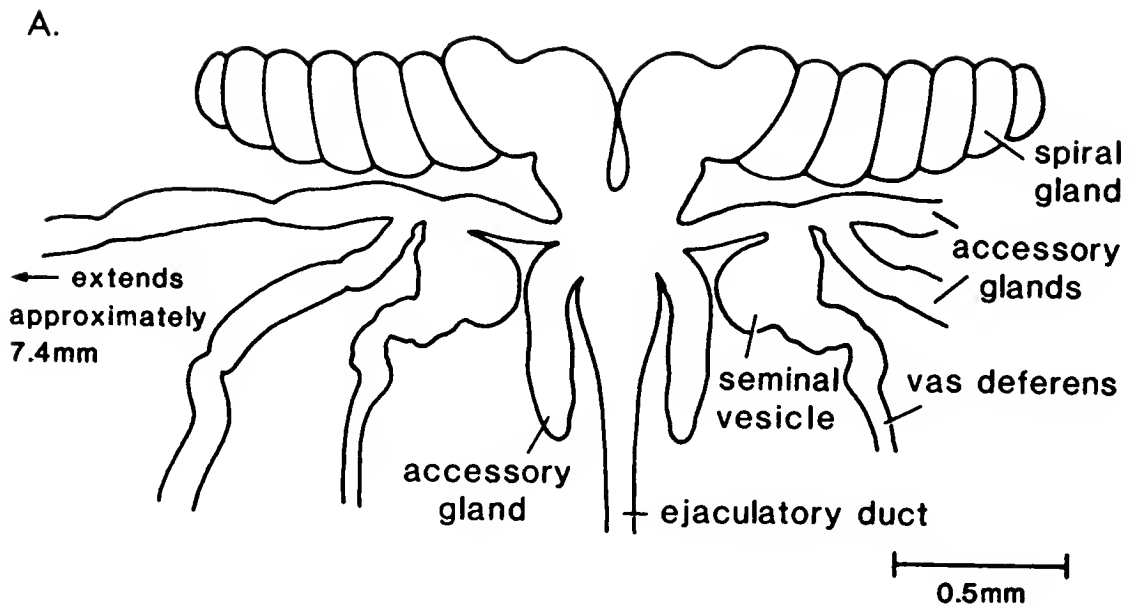seminal vesicle

accessory gland

ejaculatory duct

0.3mm

Fig. 30. <u>Photinus collustrans</u> gynandromorph.

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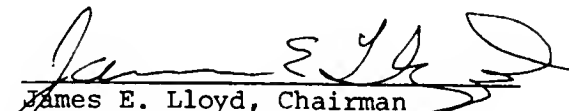
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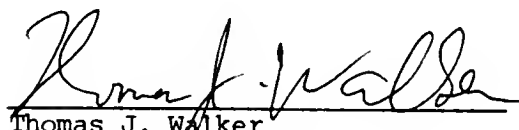
BIOGRAPHICAL SKETCH

I was born while my parents lived in married student housing at Iowa State University. My childhood was spent at an agricultural experiment station of the University of Florida. I went on to receive Bachelor of Science (1979) and Master of Science (1982) degrees from U.F. Despite having failed in my effort to finish college before my son and daughter entered it, I now hope to continue this lifelong association with educational institutions as a contributing member of the university community.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

James E. Lloyd, Chairman
Professor of Entomology and
Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.
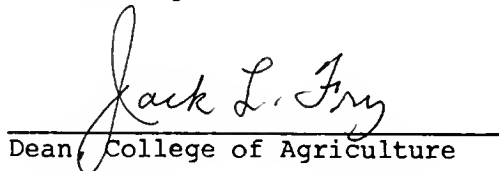
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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